

**INVESTIGATIONS INTO TEMPORAL PATTERNS  
IN DISTRIBUTION, ABUNDANCE AND HABITAT RELATIONSHIPS  
WITHIN SEABIRD COMMUNITIES  
OF THE EASTERN TROPICAL PACIFIC**

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## ABSTRACT

Of the approximately 100 seabird species recorded in the eastern tropical Pacific (ETP), nine were selected as indicators of the ecosystem, including the most abundant and widespread species in the ETP, and a diverse array of taxa and residence patterns, trophic levels, and foraging guilds. The latter is particularly relevant because four of the nine species are dependent upon the same tuna-dolphin assemblage as that targeted by the purse seine fishery, for successful foraging opportunities. These four species are referred to as “tuna-dependent” whereas the other five seabird species feed in other ways and thus are “tuna-independent.” Seabird data were collected during three years each of the Monitoring of Porpoise Stocks (MOPS) and *Stenella* Abundance Research (STAR) Projects (1988 - 1990 and 1998 - 2000, respectively) using 300 m strip transect methods. Three measures of temporal change were investigated: distribution, abundance, and habitat association patterns.

Annual distribution patterns illustrate two features. First, at a large spatial scale (the entire study area), there are distinct species-specific distributions which are consistent over time. Second, at a finer spatial scale (within a particular water mass), there is notable variation between years. Both features are evident for tuna-dependent and tuna-independent species.

Absolute abundance estimates were calculated using generalized additive models. There were no significant trends in population size for any species but the Tahiti Petrel (*Pseudobulweria rostrata*), for which a significant decline was detected. Abundance estimates fluctuated over time and the degree of variation was greater within a particular decade than between decades. These differences in population size do not represent absolute changes, but represent movement of birds into and out of the ETP from elsewhere. No differences in abundance patterns were detected for tuna-dependent *versus* tuna-independent species.

Habitat association patterns were explored using Canonical Correspondence Analysis. A series of analyses were performed with various subsets of species and habitat variables, the latter included oceanographic, geographic, and temporal variables. Three general results are relevant. First, for any given year, oceanographic and geographic variables explained between 22 and 39% of the variance in species density when all species were considered together. When considered individually, the analysis explained a high proportion of variance (25% or more and up to 89%) for four to six species, depending upon the set chosen for the analysis. Second, for those species for which the analysis explained a high proportion of variance, there were clear patterns in association with water mass types, and these association patterns remained broadly consistent across time. Within water masses, the strength of the association for any given species varied with time; this variation was higher within than between decades. Third, relative to all three types of habitat variables, oceanography and geography explained the vast majority of variance in species data. When temporal variables were incorporated into the analysis, year explained a higher proportion of variance than decade, but added less than 2% to the total variance explained as compared to a few tenths of a percent for decade.

Our general conclusions for seabirds are the following. There are clearly species-specific

associations with water mass types and these remain relatively consistent through time; temporal variation in distribution and habitat association patterns is apparent but tends to occur within a particular water mass. For any particular species, the number of individuals in the ETP fluctuates over time but, with the exception of one species, there were no temporal trends in abundance. For distribution, abundance, and habitat association patterns, temporal variation was as great within a particular decade as between decades. Finally, there were no obvious differences in any of these patterns for tuna-dependent versus tuna-independent species.

## INTRODUCTION

Seabirds are defined as birds which obtain some or all of their food from the sea; yet all must return to land to breed. Within these relatively unifying constraints, seabirds have evolved a number of life history traits in common. They are long-lived - life span is usually at least 10 years and can be as long as 60 or more; they exhibit delayed reproductive maturity - breeding never begins before age 2 y and typically ranges from 4 to 10 y or older; they have low reproductive rates - almost no oceanic species fledge more than a single chick per season, and adult mortality is low - generally less than 10% annually (Nelson 1978, Furness and Monaghan 1987, Warham 1990; 1996).

Seabirds can be useful indicator species in marine ecosystem studies because they are easily censused and because they feed at a variety of trophic levels, with different species preying upon zooplankton, micronekton, and nekton. There are approximately 200 species of seabirds in the world's oceans. During the MOPS and STAR surveys of the ETP we recorded approximately 100 species each survey year (*e.g.* Olson *et al.* 2001a). For this paper, however, we have chosen nine species/taxa to serve as indicators of the seabird community. They include the most abundant and widespread species in the ETP (King 1970, Pitman 1986; Ballance 1993; important for statistical analysis of temporal trends), comprise a diverse array of taxa (3 orders and 5 families) and residence patterns (breeding residents *versus* migrants/dispersers from outside the tropics), and represent distinct foraging guilds (Table 1).

Foraging ecology is particularly relevant to the goals of ecosystem studies within the IDCPA framework (see Ballance *et al.* 2002). Seabirds in general utilize a broad range of foraging strategies, but tropical seabirds in particular rely heavily on subsurface predators to chase prey to the surface and make it available from above. This is especially true in the ETP (Au and Pitman 1986, Ballance and Pitman 1999). The subsurface predators most often recorded in these assemblages are tunas, particularly yellowfin and skipjack (*Thunnus albacares* and *Katsuwonus pelamis*, respectively) and dolphins, particularly pantropical spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*, respectively, Au and Pitman 1986). These are the same tunas and dolphins that have been targeted by the ETP tuna purse seine fishery (see Ballance *et al.* 2002) and the seabirds that feed in this way can be used as indicators of the status of this assemblage type. Four of the nine indicator seabirds (Juan Fernandez Petrel *Pterodroma externa*, Wedge-tailed Shearwater *Puffinus pacificus*, Red-footed Booby *Sula sula*, Sooty Tern *Sterna fuscata*) are heavily dependent upon this foraging strategy (Au and Pitman 1986, Ballance *et al.* 1997). We will refer to them as “tuna-

obligate” species.

The remaining five species are not dependent upon tuna for successful foraging; we refer to them as “tuna-independent” species. They use three different foraging strategies. One is to associate directly with oceanographic features (Ballance and Pitman 1999, Ballance *et al.* 2001, Spear *et al.* 2001). Physical gradients can concentrate nutrients and therefore enhance primary production, can carry planktonic organisms through upwelling, downwelling, and convergence, and can maintain property gradients (*e.g.*, fronts) to which prey actively respond. The result is that planktonic prey are often concentrated at oceanographic features and three of the nine indicator species/taxa in this study forage in this way (Wedge-rumped Storm-petrel *Oceanodroma tethys*, Leach’s Storm-petrel *Oceanodroma leucorhoa*, Phalaropes - Northern *Phalaropus lobatus* and Red *P. fulicarius*; Spear *et al.* 2001).

The Tahiti Petrel (*Pseudobulweria rostrata*) feeds mostly alone and exclusively by scavenging on squid floating on the surface (Spear and Ainley 1998, Ballance and Pitman 1999, Ainley and Spear, unpublished data).

The White-winged Petrel (*Pterodroma leucoptera*) occasionally feeds in multi-species flocks over subsurface predators (Pitman and Ballance, unpublished data), but also appears to feed at night or crepuscularly, and takes mainly myctophids (Ainley and Spear, unpublished data).

In summary, the seabird indicator species/taxa we chose include four abundant species that are heavily dependent upon tunas and dolphins for successful feeding opportunities, and five species/taxa that feed in other ways and are largely independent of tuna-dolphin assemblage dynamics.

To investigate temporal patterns in the seabird community, we use three measures: distribution, abundance, and habitat relationships. These investigations and analyses are to be interpreted within the context of the International Dolphin Conservation Program Act (ICPA). Relevant background information can be found in Ballance *et al.* (2002).

An independent scientific peer review of this work was administered by the Center for Independent Experts located at the University of Miami. Responses to reviewer’s comments can be found in Appendix 3.

**Table 1.** Indicator species/taxa used in this study. References: Harrison (1983), Harrison *et al.* (1983), Au and Pitman (1986), Pitman (1986), Pitman and Ballance (1990), Spear and Ainley (1998), Ballance and Pitman (1999), Spear *et al.* (2001), and our unpublished observations.

Species	Geographic Distribution in the Pacific Ocean	Order and Family	Prey Type	Foraging Behavior in the eastern tropical Pacific
Tahiti Petrel <i>Pseudobulweria rostrata</i>	- Breeds in south central tropical Pacific - Non-breeding dispersal throughout tropical Pacific but primarily east of 170° W	Procellariiformes Procellariidae	Squid	Scavenge (tuna-independent)
Juan Fernandez Petrel <i>Pterodroma externa</i>	- Breeds in temperate latitudes on Juan Fernandez Islands, Chile - Non-breeding migration throughout eastern tropical Pacific	Procellariiformes Procellariidae	Nekton: fish and squid	Multispecies flocks with subsurface predators (tuna-dependent)
White-winged Petrel <i>Pterodroma leucoptera</i>	- Breeds in southwest tropical Pacific - Non-breeding migration throughout eastern tropical Pacific	Procellariiformes Procellariidae	Micro-nekton: primarily myctophids Some plankton	Possibly nocturnal or crepuscular foragers; Occasionally feeds diurnally in multispecies flocks with subsurface predators (tuna-independent)
Wedge-tailed Shearwater <i>Puffinus pacificus</i>	- Breeds throughout tropical Pacific and Indian oceans - Ranges widely during non-breeding period but confined to tropical waters	Procellariiformes Procellariidae	Nekton: fish and squid	Multispecies flocks with subsurface predators (tuna-dependent)
Wedge-rumped Storm-petrel <i>Ocenodroma tethys</i>	- Restricted to eastern tropical Pacific and Peru Current	Procellariiformes Oceanitidae	Plankton and micro-nekton (primarily myctophids)	Associate with oceanographic features (tuna-independent)

Leach's Storm-petrel <i>Oceanodroma leucorhoa</i>	<ul style="list-style-type: none"> <li>- Breeds in temperate latitudes throughout northern Pacific</li> <li>- Non-breeding migration throughout tropics</li> </ul>	Procellariiformes Oceanitidae	Plankton and micro-nekton (primarily myctophids)	Associate with oceanographic features (tuna-independent)
Red-footed Booby <i>Sula sula</i>	<ul style="list-style-type: none"> <li>- Pantropical</li> <li>- Adults largely sedentary around breeding colonies</li> </ul>	Pelecaniformes Sulidae	Nekton: fish and squid	Multispecies flocks with subsurface predators (tuna-dependent)
Phalarope species Northern: <i>Phalaropus lobatus</i> Red: <i>Phalaropus fulicarius</i>	<ul style="list-style-type: none"> <li>- Breeding distribution circumpolar on continental mainlands</li> <li>- Non-breeding migration mainly to coastal tropical areas</li> </ul>	Charadriiformes Phalaropodidae	Plankton	Associate with oceanographic features (tuna-independent)
Sooty Tern <i>Sterna fuscata</i>	<ul style="list-style-type: none"> <li>- Pantropical</li> <li>- Disperses widely during non-breeding season</li> </ul>	Charadriiformes Laridae	Nekton: fish and squid	Multispecies flocks with subsurface predators (tuna-dependent)

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## DATA COLLECTION METHODS

### *Seabird Data*

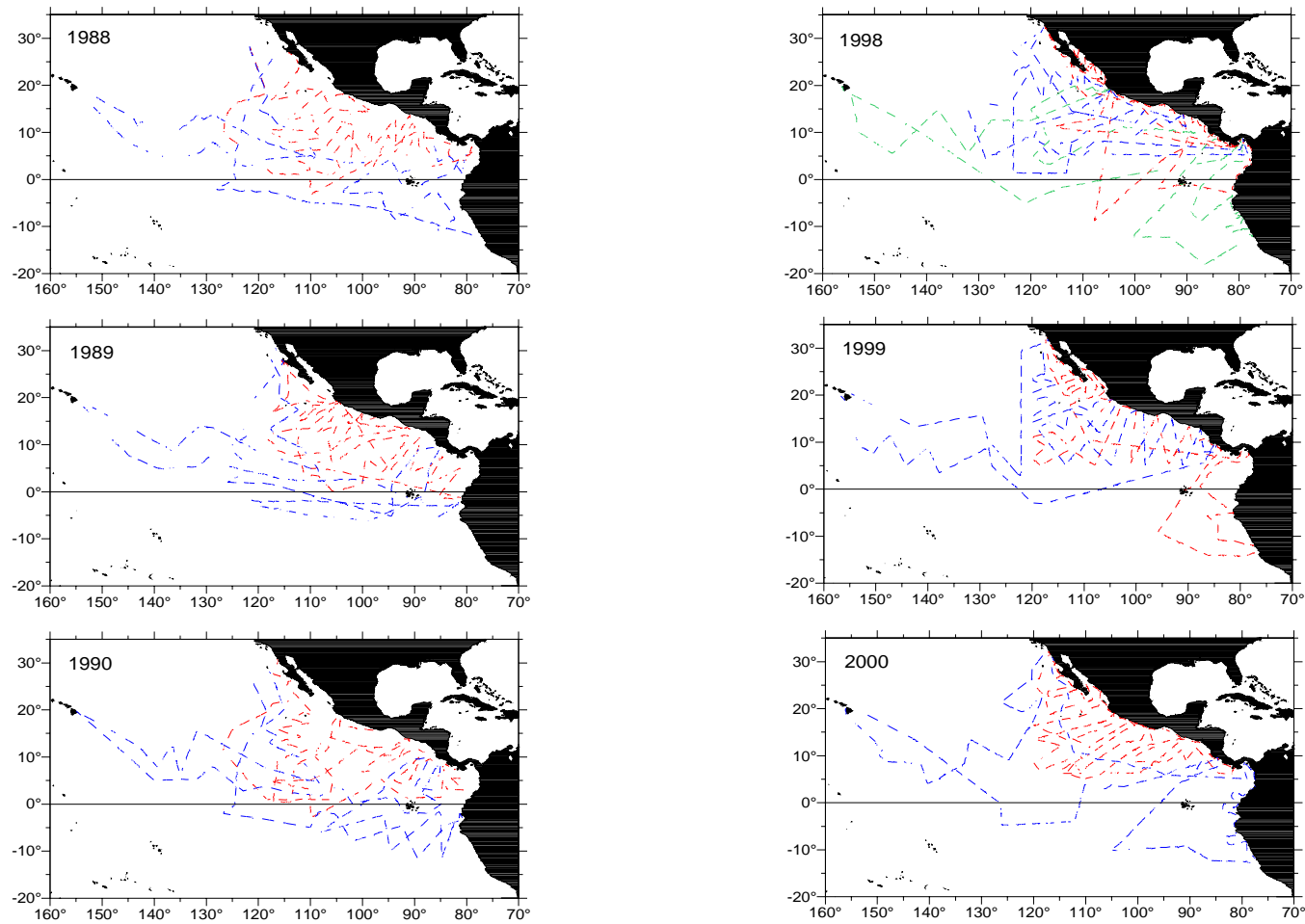
Seabird data were collected using standard strip transect methods, whereby all birds entering a designated quadrant of the ship, from bow to beam on one side only, are recorded continuously. We used a default strip width of 300 m. Because this survey method assumes all birds are detected, we adjusted strip width to 200 m at times for smaller species only (storm-petrels and phalaropes) to reflect visibility conditions. Range finders were constructed following methods outlined in Heinemann (1981) and were used throughout the cruises by all observers to calibrate distance from the ship.

Two observers rotated through two-hour shifts with a single observer on effort during any particular time. Effort was maintained during all daylight hours, weather permitting, when the ship was underway. Effort was suspended when an observer did not feel confident that all birds entering the strip could be detected; this generally occurred at sea states of Beaufort 6 (winds higher than 21 knots = 39 km/h) and higher.

For all birds, we recorded species identification, number of individuals, and behavior (feeding, flying, or sitting). Prior to analysis, we excluded all ship followers from the data; their inclusion would result in artificially inflated seabird density values. Age (juvenile, adult) and sex were recorded when possible.

Seabird data are available for three of the six MOPS years: 1988, 1989, and 1990, and for all three STAR years (1998 - 2000). Figure 1 illustrates geographical distribution of survey effort on a yearly basis throughout the study area.

**Figure 1.** On-effort survey periods during which seabird data were collected. Colors represent ship-specific tracklines: blue = *McArthur*; red = *David Starr Jordan*; green = *Endeavor* (1998 only).



## *Oceanographic Data*

Oceanographic data were collected aboard all ships simultaneously with seabird data. Sea surface temperature and salinity were measured continuously with a flow-through thermosalinograph. Expendable bathythermograph drops to 760 m were made daily at 0900, 1200, and 1500. Conductivity, temperature and depth casts to 1000 m were made each morning and evening approximately one hour before and one hour after daylight. Further details regarding data collection, data processing, and sample sizes are given in Fiedler and Philbrick (2002).

## **ANALYSES AND RESULTS**

For all analyses that follow we chose a single survey day, approximately 100 nautical miles of trackline (185 km), as our sampling unit. Area surveyed per day ranged from 0.6 (1989) to 78.7 (2000) km<sup>2</sup>. Daily values of seabird density were calculated from daily totals of birds sighted and area surveyed. This choice of sampling unit size was based upon the fact that daily variation in the oceanic habitat of the pelagic ETP (as defined by the oceanographic variables used here) averaged an order of magnitude less than the variation in these parameters over the entire study area (see figures in Fiedler *et al.* 1991). This same spatial and temporal scale has been used successfully in previous analyses of ETP oceanography, seabirds, and cetaceans (Reilly and Fiedler 1994, Ballance *et al.* 1997).

Table 2 gives sample size information for each of the indicator species for each survey year. These data form the basis for the following results.

**Table 2.** Total number of ship days during which seabirds were censused and total number of birds recorded on effort by species and year. Note that numbers recorded are not necessarily proportional to abundance when compared across years (see Results: Population Abundance and Trends).

	<b>1988</b> 194 days	<b>1989</b> 204 days	<b>1990</b> 209 days	<b>1998</b> 293 days	<b>1999</b> 215 days	<b>2000</b> 221 days	<b>Total</b> 1,336 days
<b>Tahiti Petrel</b>	114	177	150	213	209	159	1,022
<b>Juan Fernandez Petrel</b>	1,762	2,108	3,403	2,879	3,591	3,012	16,755
<b>White-winged Petrel</b>	122	238	285	42	155	155	997
<b>Wedge-tailed Shearwater</b>	726	964	1,261	1,269	1,940	1,092	7,252

<b>Wedge-rumped Storm-petrel</b>	621	973	767	1,291	858	874	5,384
<b>Leach's Storm-petrel</b>	928	1,730	1,524	2,838	1,971	2,036	11,027
<b>Red-footed Booby</b>	342	307	652	291	396	280	2,268
<b>Phalarope species</b>	635	1,004	1,621	2,953	1,362	7,398	14,973
<b>Sooty Tern</b>	427	484	110	310	452	409	2,192
<b>Total</b>	5,677	7,985	9,773	12,086	10,934	15,415	61,870

## I. DISTRIBUTION

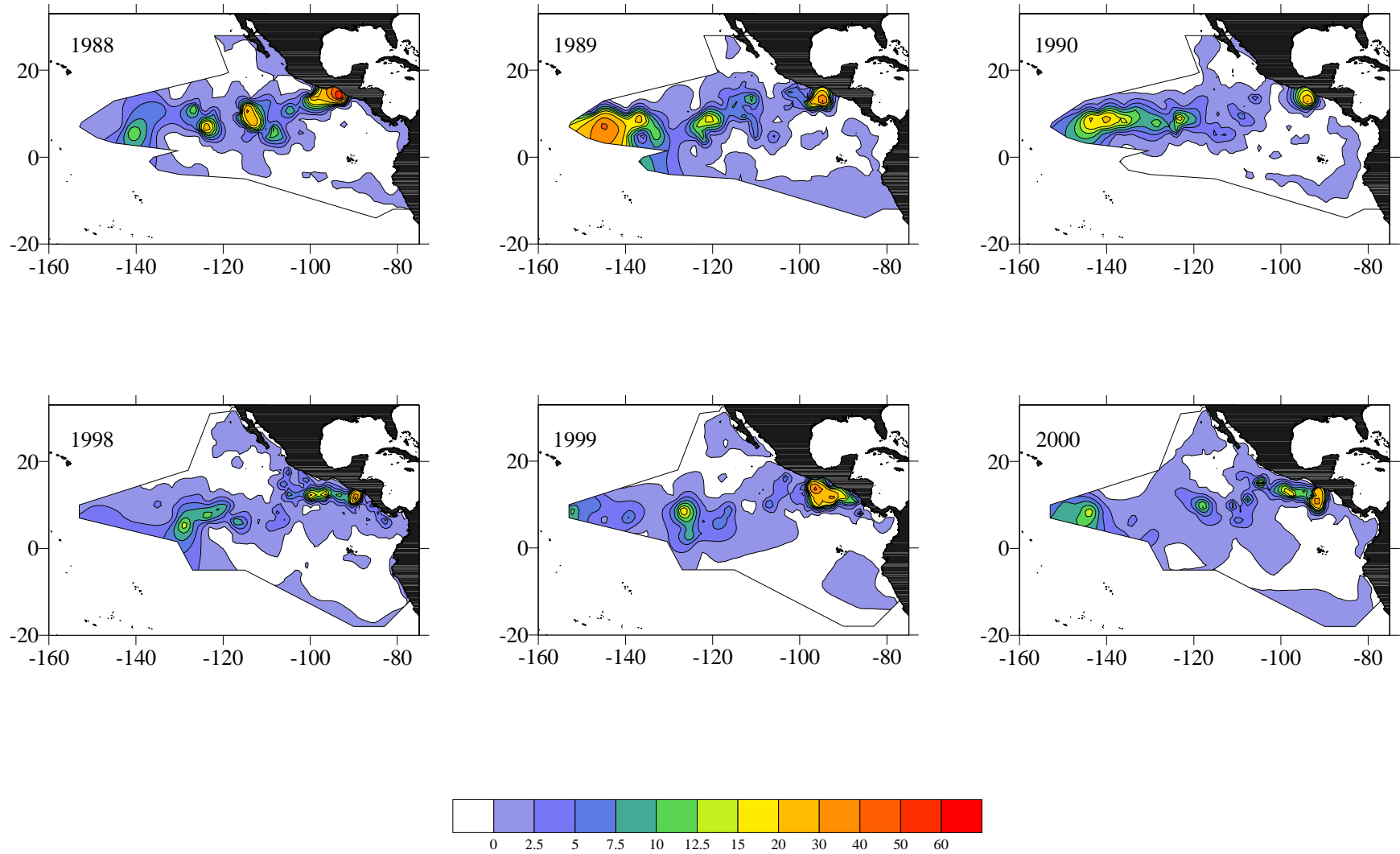
### *Analyses*

Daily density values were standardized to birds recorded per 100 km<sup>2</sup> per day. Distribution plots with resulting daily densities were made using the software program *Surfer 7*. We used the default option of kriging for contouring density values. This method does not extrapolate using variables related to density, but instead, simply draws contours to account for known density values. Generalized additive models provide a more accurate depiction of distribution (see Results: Population Abundance and Trends and figures 11 and 12) and will be used to produce distribution plots in our subsequent paper.

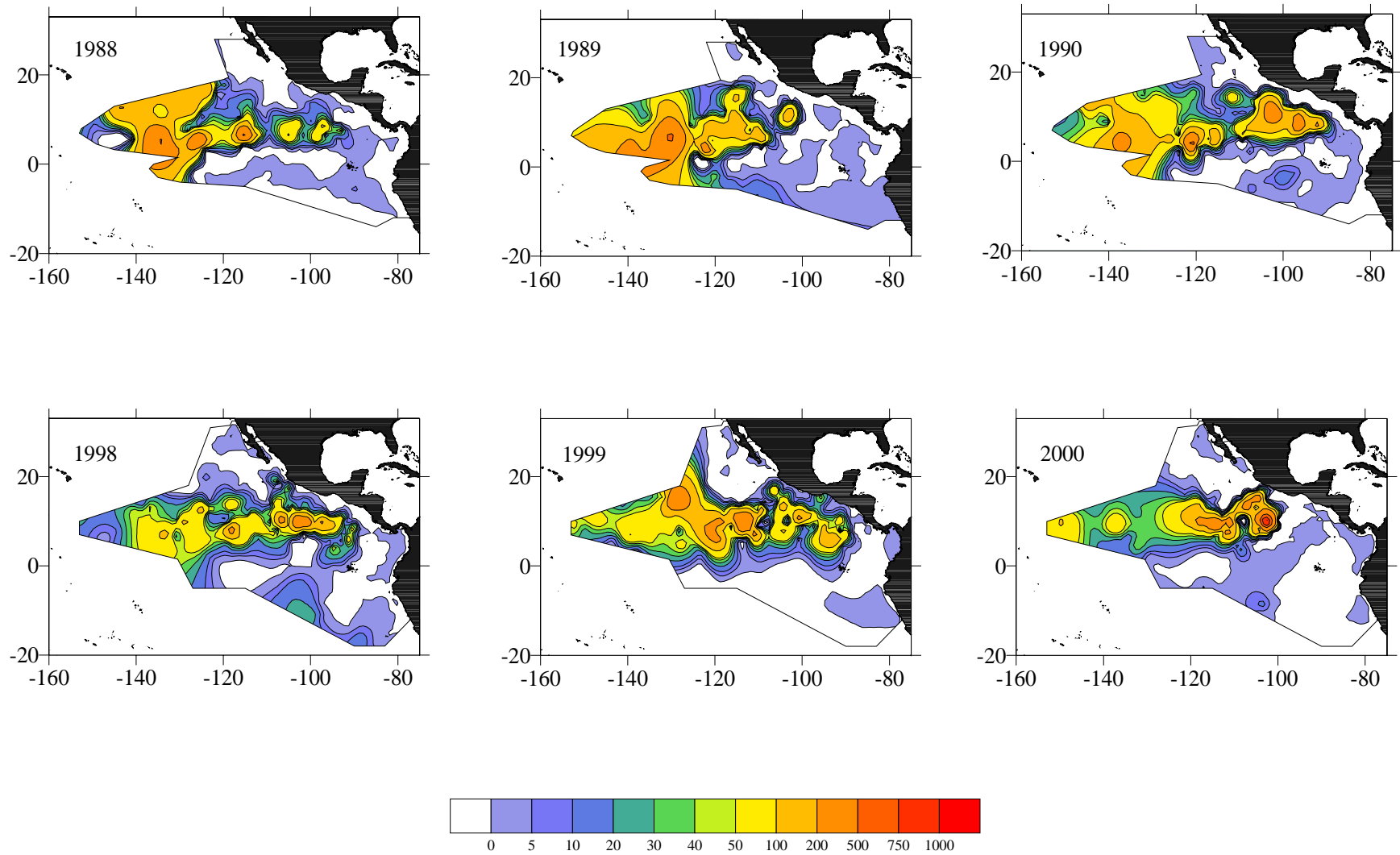
### *Results and Discussion*

Yearly distribution patterns for the nine indicator species are illustrated in Figures 2 - 10. Two features are immediately apparent. First, across all years, species-specific distribution patterns are quite pronounced. Second, there is notable interannual variation in distribution within each species.

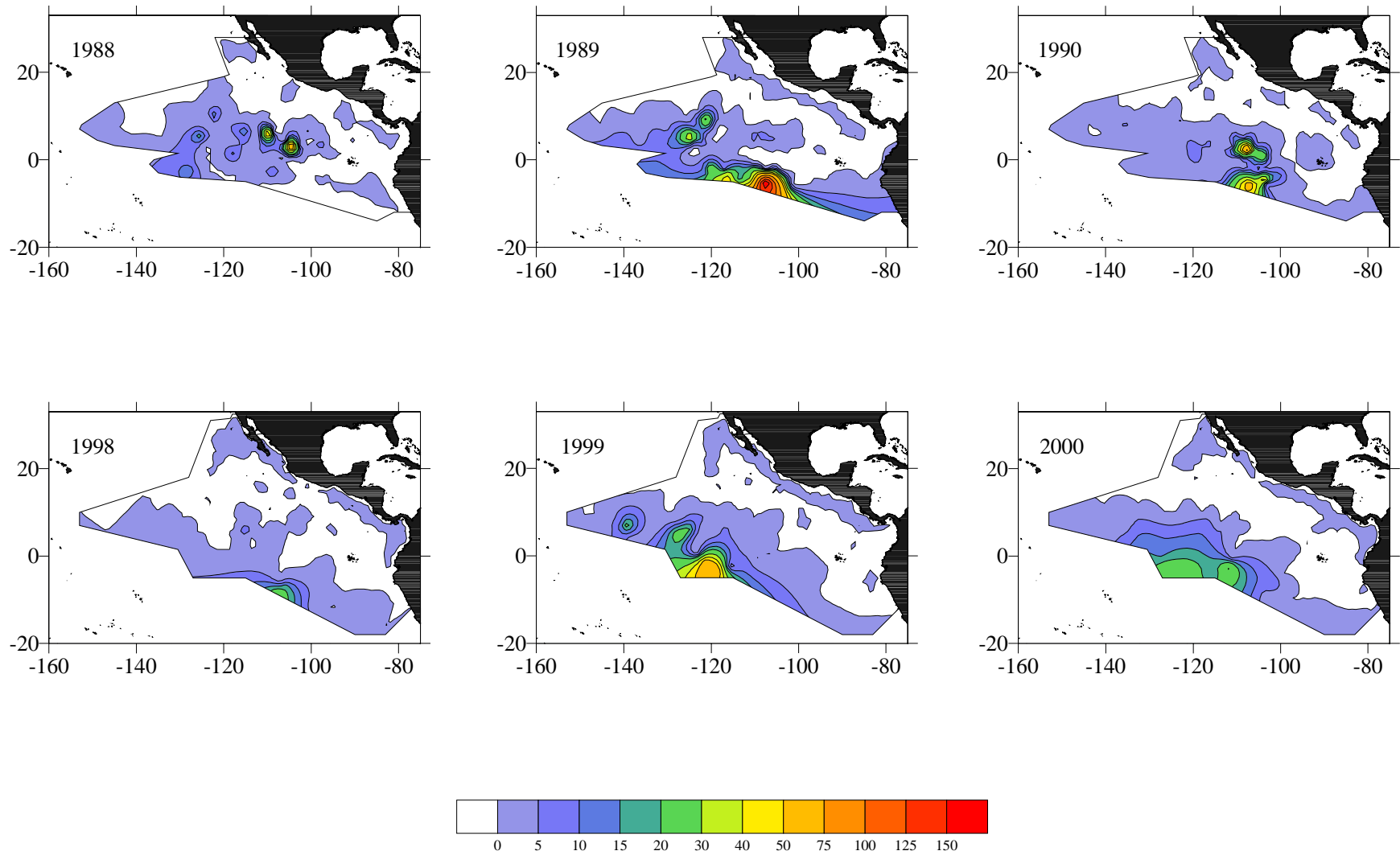
**Figure 2.** Tahiti Petrel distribution. Color contours represent birds per 100 km<sup>2</sup> per day.



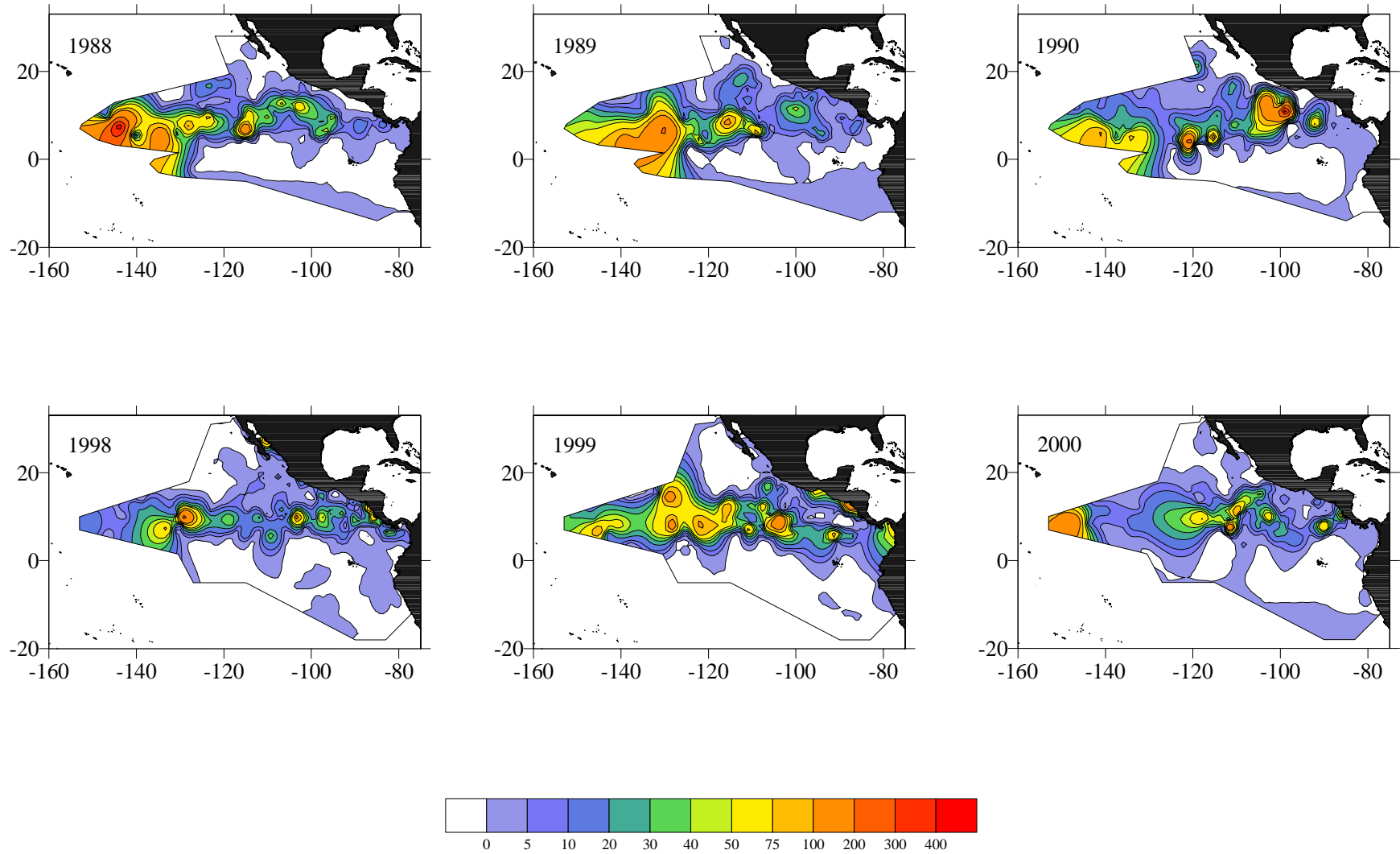
**Figure 3.** Juan Fernandez Petrel distribution. Color contours represent birds per 100 km<sup>2</sup> per day.



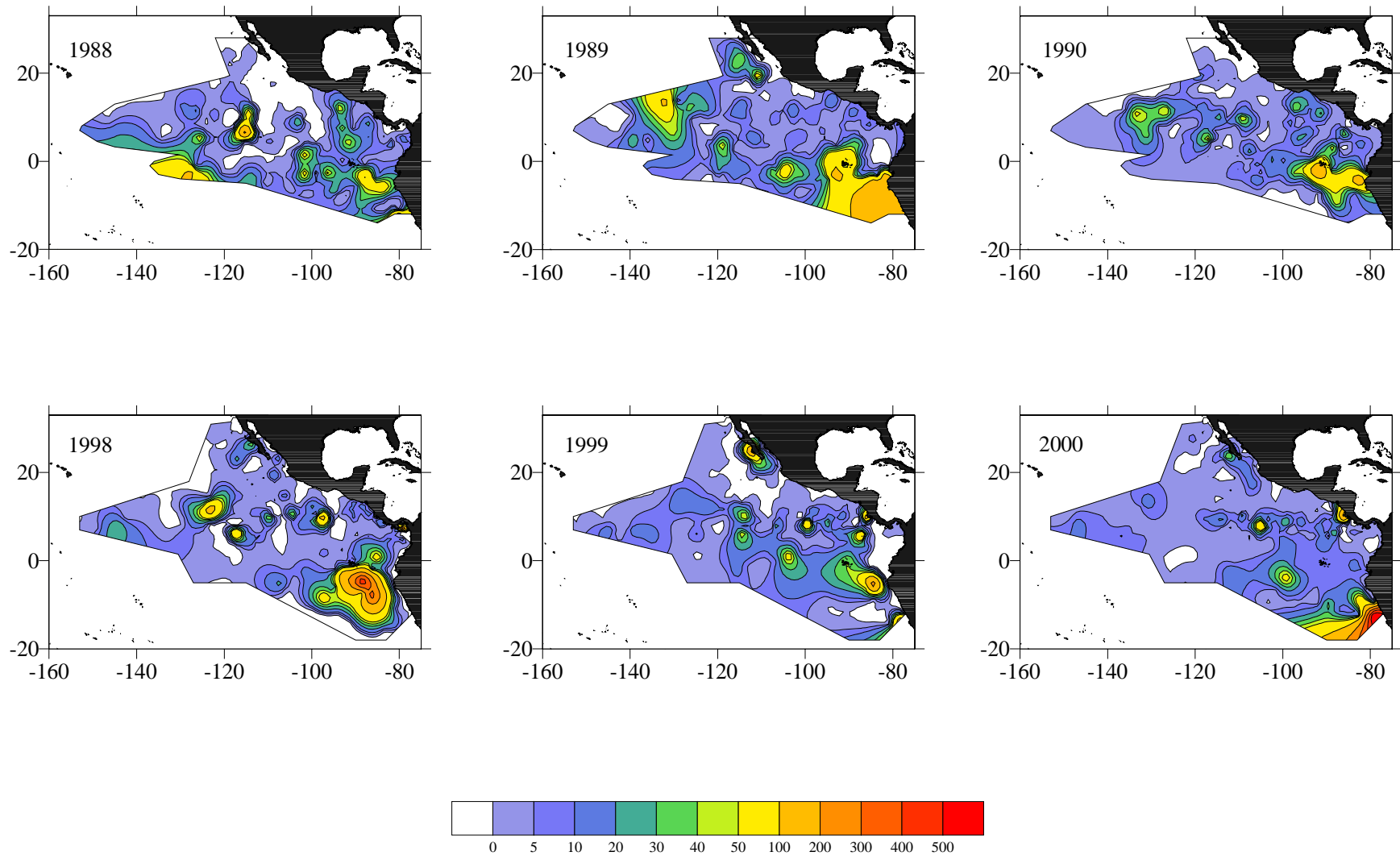
**Figure 4.** White-winged Petrel distribution. Color contours represent birds per 100 km<sup>2</sup> per day.



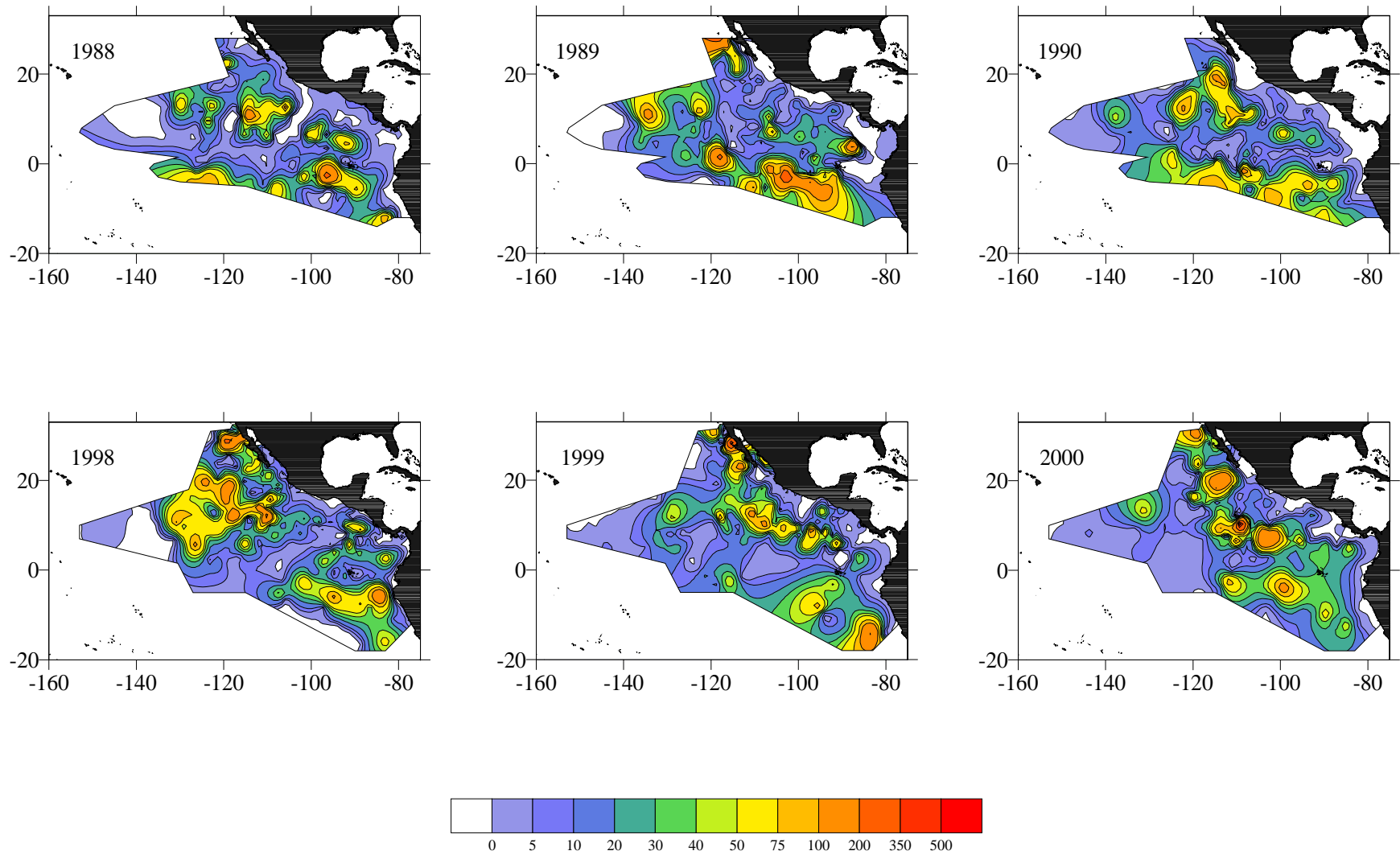
**Figure 5.** Wedge-tailed Shearwater distribution. Color contours represent birds per 100 km<sup>2</sup> per day.



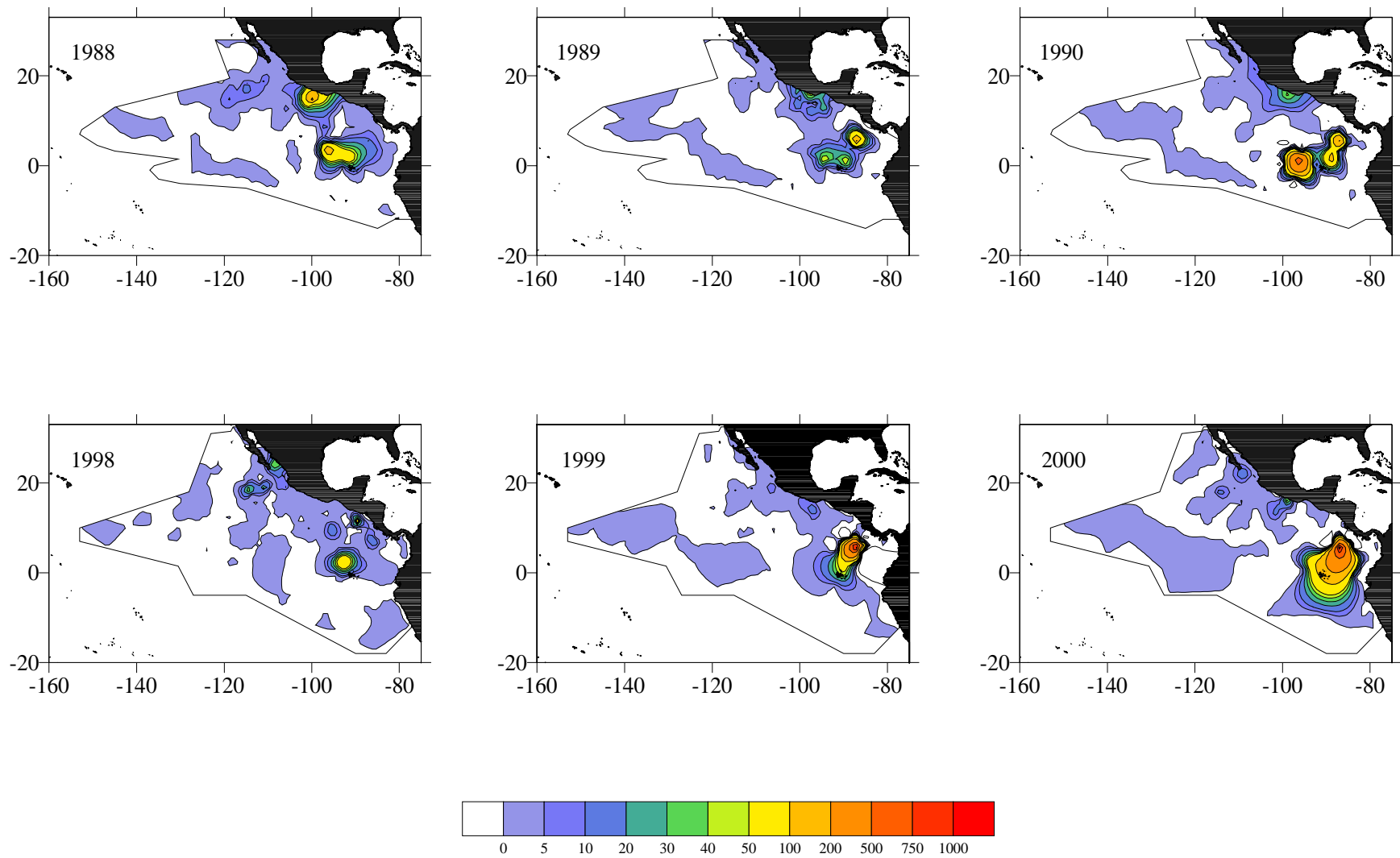
**Figure 6.** Wedge-rumped Storm-petrel distribution. Color contours represent birds per 100 km<sup>2</sup> per day.



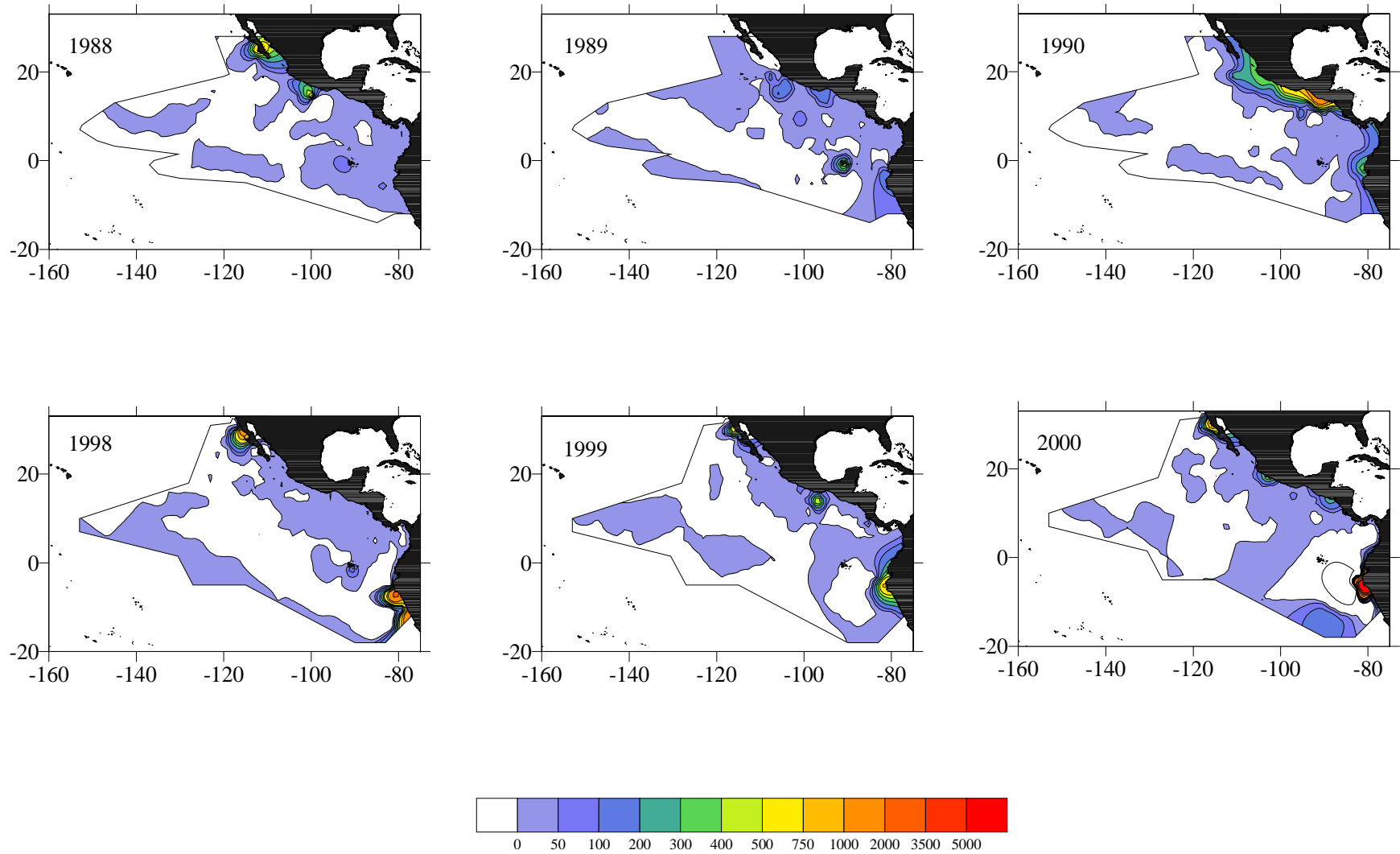
**Figure 7.** Leach's Storm-petrel distribution. Color contours represent birds per 100 km<sup>2</sup> per day.



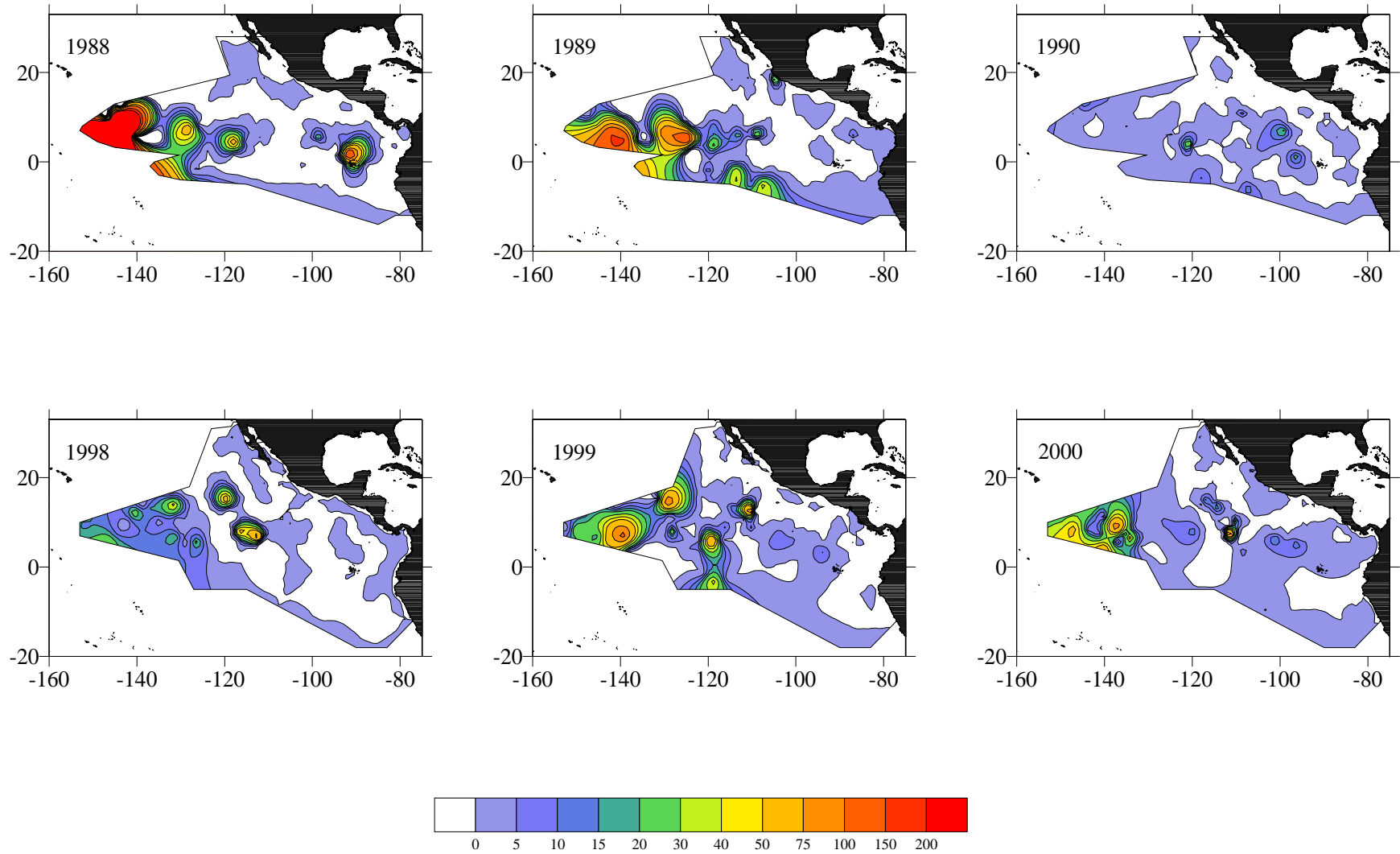
**Figure 8.** Red-footed Booby distribution. Color contours represent birds per 100 km<sup>2</sup> per day.



**Figure 9.** Phalarope species distribution. Color contours represent birds per 100 km<sup>2</sup> per day.



**Figure 10.** Sooty Tern distribution. Color contours represent birds per 100 km<sup>2</sup> per day.



## II. ABUNDANCE

### *Analyses*

We used generalized additive models (GAMs: see Hastie and Tibshirani 1990, Clarke *et al.* in review) to examine abundance and trends in abundance of each seabird species. GAMs were chosen because they were designed to deal with nonrandom survey effort (including under-surveyed areas) in combination with nonrandom distribution of species. GAMs, being model- rather than sample-based, overcome such biases. They also capture complex nonlinear trends in density while using only a few parameters. Specifically, only four independent variables (latitude, longitude, ocean depth, distance to the mainland) were initially included in each analysis. Therefore, besides increasing the accuracy, with small values of degrees of freedom they considerably improve the precision of abundance estimates among marine biota (compared to previously used analytical procedures), which usually have extremely variable (clumped) densities over their pelagic ranges (*e.g.*, Hunt 1990).

The dependent term used in these models was seabird density and the sample unit was one "transect day" in which  $>10\text{km}^2$  of ocean area was surveyed. (Days in which  $<10\text{ km}^2$  of area was surveyed were excluded from these analyses.) For each of the four tuna-dependent species the areas surveyed per day averaged  $45.1 \pm 13.4\text{ km}^2$ , range = 10.5 to  $78.8\text{ km}^2$ ,  $n = 1297$  days, and survey effort for the five tuna-independent species averaged  $39.6 \pm 12.1\text{ km}^2$ , range = 10.1 to  $77.9\text{ km}^2$ ,  $n = 1281$  days. The reason for the difference between the two groups is that survey strip-width, and thus area surveyed, was reduced for the smaller, tuna-independent species compared to the larger, tuna-dependent species when visibility conditions were less than optimal. Seabird densities per day were weighted by ocean area surveyed to control for differences in area surveyed per day.

Because we wanted to obtain population estimates that were as close as possible to true estimates of bird abundance, raw seabird densities recorded during surveys were corrected for the effect of flight speed relative to ship speed (Spear *et al.* 1992; flight speeds in Spear & Ainley 1997). To accomplish this we adjusted densities using "correction factors" (Spear & Ainley, unpublished data) that had been determined for each study species during surveys conducted in a separate study (*e.g.*, see Spear *et al.* 2001). Correction factors were estimated using only those data collected during which ship speeds were similar to that during MOPS and STAR (10 knots). Without these corrections, densities from at-sea survey data tend to be overestimated for birds that fly faster than the vessel, and underestimated for birds that fly slower. The correction also is required because any patterns in bird/ship direction will bias analyses. For example, if birds flew north and south at the same speed and in equal numbers, uncorrected counts from a ship transiting north would falsely indicate greater numbers flying south.

### *Results and Discussion*

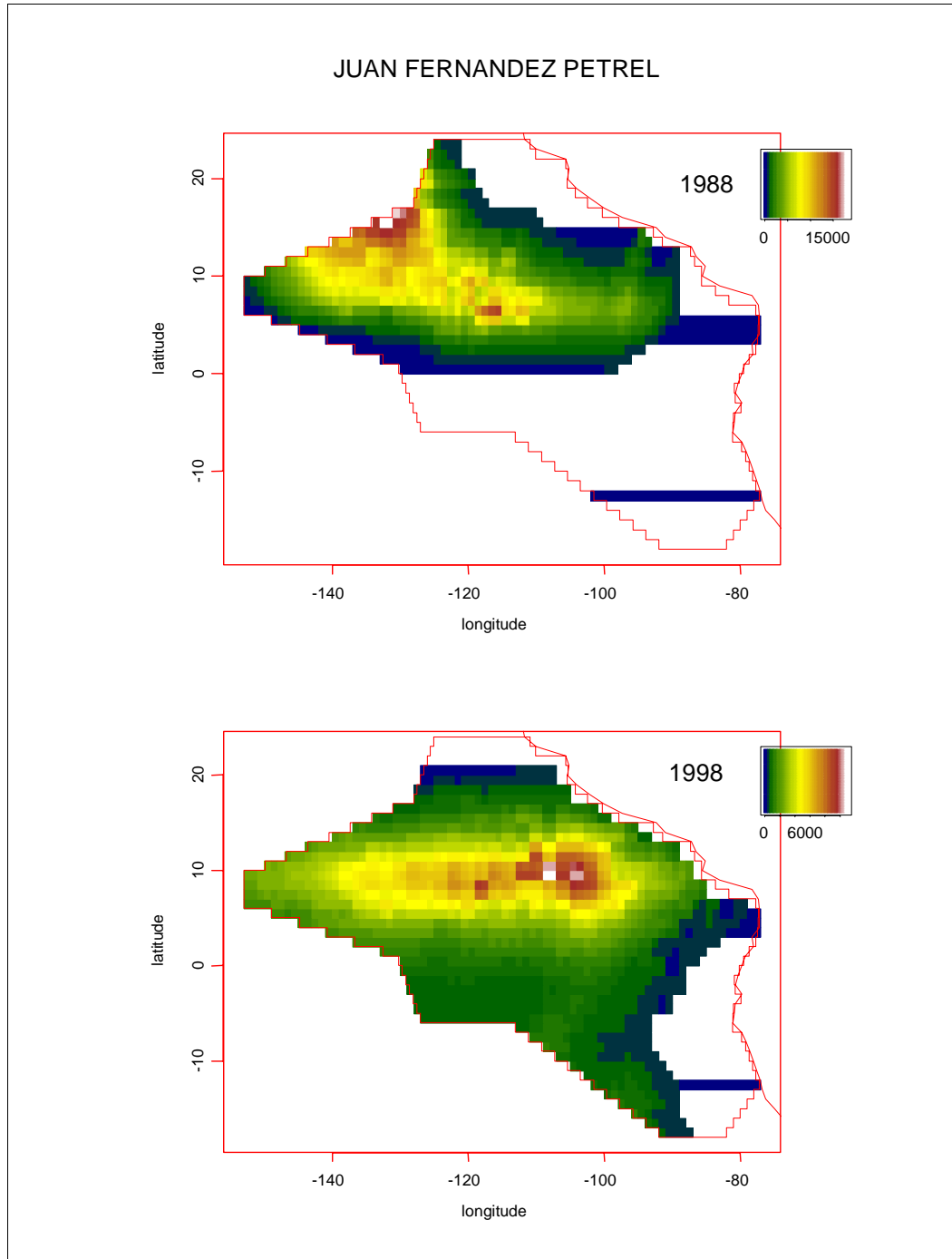
GAMs Modeling - Precision and Accuracy. Figures 11 and 12 show examples of annual distributions in two years for two of the study species plotted using GAMs. Coefficients of variation (CVs) for the annual point estimates, averaged among each species, ranged from 9.3 to 19.1,

however, mean CVs of six of the nine species were less than 12.0 (Table 3). Based on these results, the GAMs performed well in modeling the distributions and estimating population sizes. The species with the largest CVs were the White-winged Petrel and Red / Red-necked Phalaropes; they were more difficult to model due to their highly clumped occurrence patterns across their ranges in any given year (not shown). As noted above, the CVs (as well as the 95% CIs) shown in Table 3 were those resulting from the point estimate analyses in which one analysis was conducted for each year. The smoothed CIs and CVs, which are a result of the trends analyses in which a final bootstrap using year as the only dependent variable, are not shown in these preliminary results. However, these are generally about half the size of those calculated during the point estimate analyses.

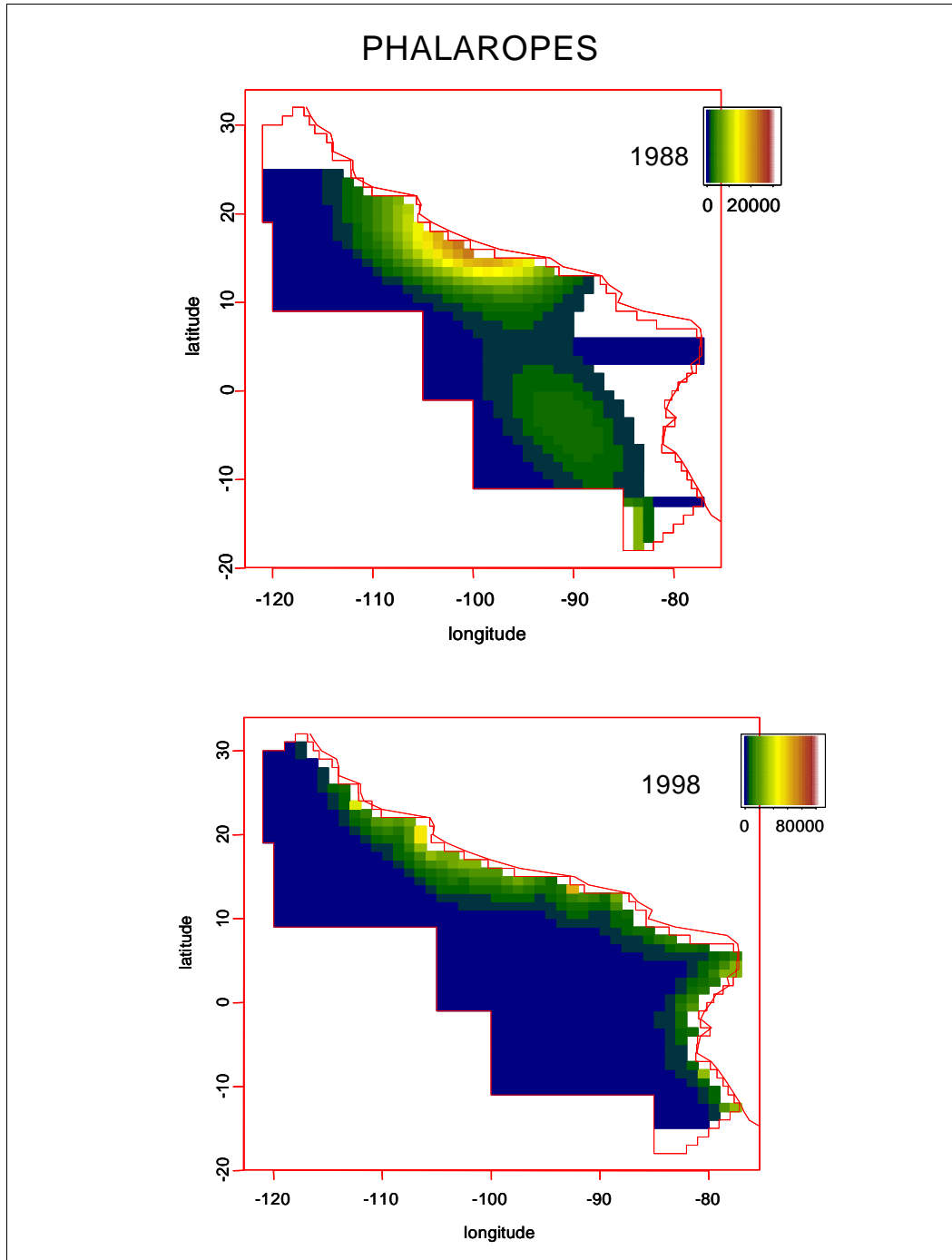
Accuracy of the population estimates is difficult to assess, however, assuming that standardization of survey methods was maintained throughout the study, we suspect that they are probably accurate within 10%. Our basis for this rests on the results from previous analyses (Clarke *et al.* in review) in which we compared abundance estimates obtained during at-sea surveys with independent estimates obtained during colony-based surveys for three species: the Waved Albatross (*Phoebastria irrorata*) that breeds on the Galapagos Islands, and the Western Gull (*Larus occidentalis*) and Common Murre (*Uria aalge*) populations that breed on the Farallon Islands. Comparisons between the sea-based and colony-based estimates were surprisingly close, and for the three species varied by only a few percent in each case. In addition, the colony-based estimates for two of these species, the gull and murre, for which 10 years of at-sea and colony based estimates were available for each species, fell mostly within the confidence intervals for the at-sea estimates.

The only species in this study for which we have an independent estimate is the Juan Fernandez Petrel, for which a colony-based estimate of 1 million breeding pairs (this species breeds on a single island in the Juan Fernandez archipelago off Chile) was obtained in 1986 (Brooke 1987). Based on the estimate of ca. 2 million breeding petrels and additional information indicating that breeding numbers of these long lived, K-selected seabirds usually includes approximately 50% of the total population, we would expect a population size for this species of 4 million birds total. This estimate lies reasonably close to the yearly average (4,208,000 birds) for the at-sea estimates obtained in this study.

**Figure 11.** GAMs plots for the distribution of Juan Fernandez Petrel during 1988 and 1998. Grids are  $1^\circ$  by  $1^\circ$  square.



**Figure 12.** GAMs plots for the distribution of phalaropes (Red and Red-necked) during 1988 and 1998.



**Table 3.** Annual population estimates, 95% confidence intervals, and coefficients of variation (CV) for nine species of seabirds during six survey years.

Year	Pop. Est.	95% CI	CV
Juan Fernandez Petrel			
1988	3,350,000	2,128,000 - 3,477,000	10.1
1989	5,142,000	4,231,000 - 6,719,000	11.6
1990	4,906,000	4,105,000 - 5,877,000	9.3
1998	3,364,000	2,892,000 - 3,967,000	8.0
1999	4,786,000	4,008,000 - 5,828,000	8.5
2000	3,701,000	3,020,000 - 4,623,000	11.9
AVE.	4,208,000	3,397,000 - 5,081,000	9.9
Wedge-tailed Shearwater			
1988	1,717,000	1,344,000 - 2,269,000	12.7
1989	3,037,000	2,652,000 - 3,856,000	9.6
1990	2,529,000	1,871,000 - 3,059,000	12.4
1998	1,614,000	1,312,000 - 2,164,000	13.0
1999	2,819,000	2,412,000 - 3,504,000	9.2
2000	1,653,000	1,384,000 - 2,077,000	10.7
AVE.	2,228,000	1,829,000 - 2,822,000	11.3
Red-footed Booby			
1988	426,000	367,000 - 515,000	8.8
1989	259,000	213,000 - 297,000	8.0
1990	609,000	519,000 - 714,000	7.9
1998	169,000	129,000 - 202,000	11.1
1999	343,000	320,000 - 424,000	8.0
2000	497,000	327,000 - 574,000	12.2
AVE.	384,000	313,000 - 454,000	9.3
Sooty Tern			
1988	946,000	705,000 - 1,246,000	13.9
1989	2,445,000	1,971,000 - 3,145,000	12.7
1990	277,000	179,000 - 392,000	18.5
1998	644,000	526,000 - 813,000	11.0
1999	1,508,000	1,014,000 - 1,622,000	10.7
2000	1,023,000	896,000 - 1,503,000	16.0
AVE.	1,141,000	882,000 - 1,454,000	13.8

(Table 3 – continued)

Year	Pop. Est.	95% CI	CV
White-winged Petrel			
1988	517,000	311,000 - 865,000	30.3
1989	2,101,000	1,496,000 - 2,427,000	10.7
1990	620,000	496,000 - 867,000	24.3
1998	145,000	73,000 - 269,000	35.1
1999	812,000	687,000 - 1,045,000	9.3
2000	666,000	578,000 - 714,000	4.9
AVE.	810,000	610,000 - 1,031,000	19.1
Tahiti Petrel			
1988	399,000	258,000 - 416,000	11.9
1989	568,000	475,000 - 821,000	15.4
1990	345,000	276,000 - 385,000	8.0
AVE.	437,000	336,000 - 541,000	11.8
1998	267,000	208,000 - 312,000	9.2
1999	314,000	247,000 - 345,000	8.2
2000	264,000	199,000 - 319,000	11.8
AVE	282,000	218,000 - 325,000	9.7
Galapagos Storm-petrel			
1988	2,814,000	2,130,000 - 3,322,000	10.6
1989	3,995,000	3,151,000 - 4,934,000	11.1
1990	2,207,000	1,864,000 - 2,545,000	7.6
1998	4,059,000	2,927,000 - 4,549,000	9.9
1999	2,249,000	1,774,000 - 3,030,000	14.7
2000	2,325,000	1,949,000 - 3,039,000	12.1
AVE.	2,942,000	2,299,000 - 3,570,000	11.0
Leach's Storm-petrel			
1988	3,618,000	3,072,000 - 4,667,000	11.0
1989	7,862,000	6,523,000 - 9,508,000	9.2
1990	5,383,000	4,483,000 - 6,415,000	8.7
1998	5,349,000	4,777,000 - 6,244,000	7.4
1999	5,289,000	4,004,000 - 6,758,000	13.2
2000	4,770,000	3,941,000 - 5,828,000	9.5
AVE.	5,379,000	4,422,000 - 6,570,000	9.8

(Table 3 – continued)

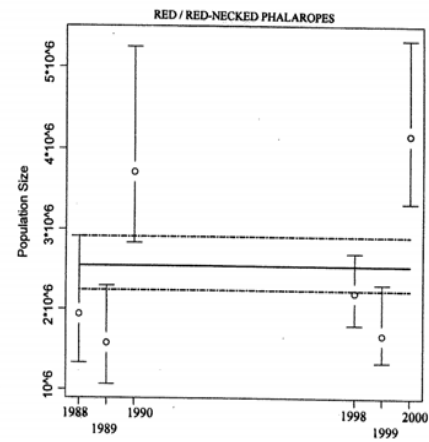
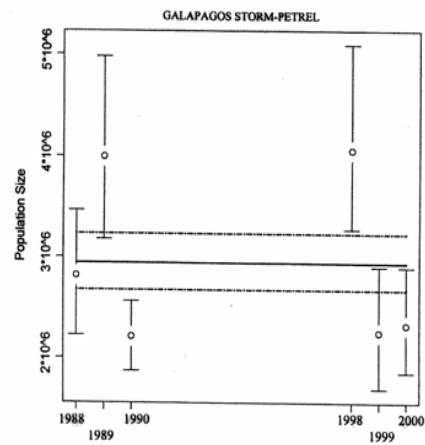
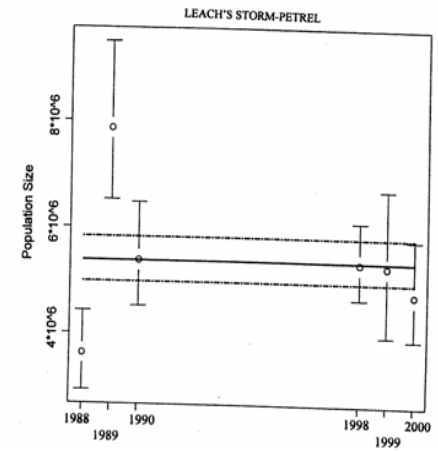
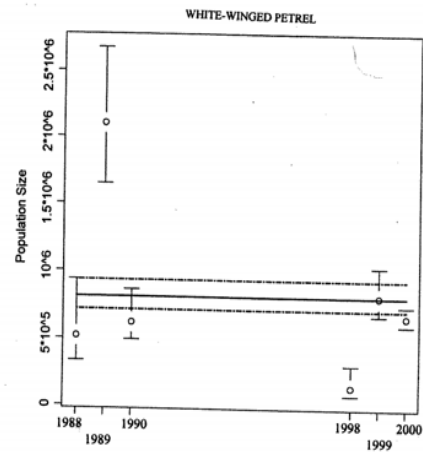
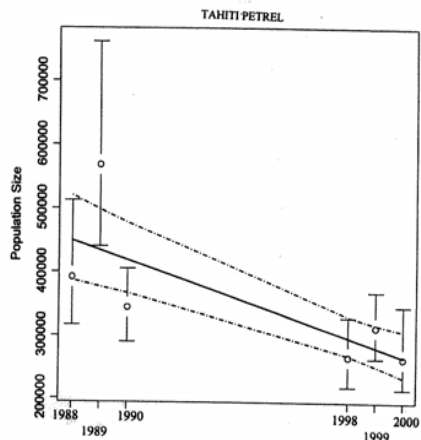
Year	Pop. Est.	95% CI	CV
Red / Red-necked Phalarope			
1988	1,939,000	1,471,000 - 3,223,000	22.9
1989	1,577,000	1,083,000 - 2,335,000	19.8
1990	3,713,000	2,747,000 - 5,079,000	15.8
1998	2,207,000	2,152,000 - 3,221,000	12.5
1999	1,680,000	1,386,000 - 2,934,000	15.2
2000	4,166,000	4,070,000 - 6,511,000	15.3
AVE.	2,547,000	2,152,000 - 3,884,000	16.9

### *Population Trends*

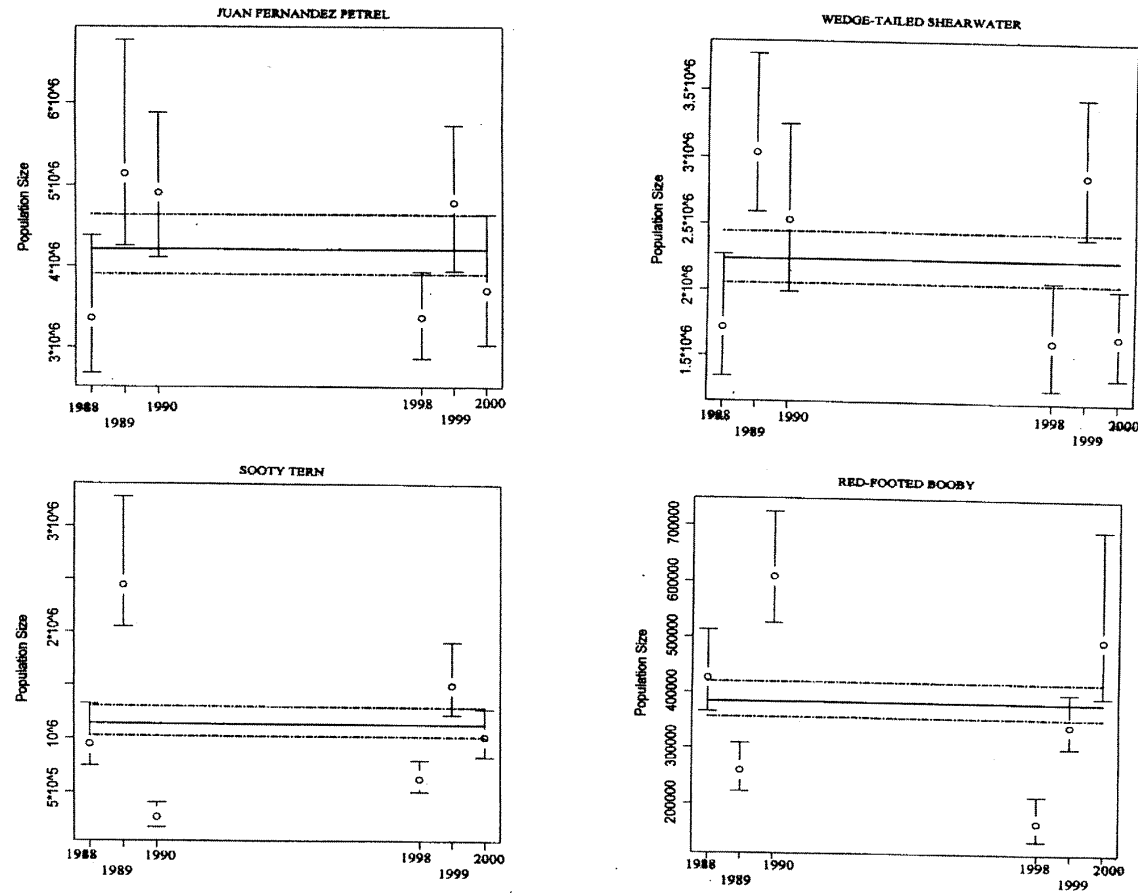
There were no significant linear or quadratic trends among the four tuna-dependent species (Table 3, Figure 13). Population estimates for the Juan Fernandez Petrel and Wedge-tailed Shearwater were lowest in the two La Niña years (1988 and 1998), and those of the Sooty Tern and Red-footed Booby showed similar trends. The four tuna-dependent species rely to a large extent on schooling yellowfin tuna that make prey available to them when the former force the prey to the ocean surface when foraging. The tuna themselves appear to be most successful in finding their prey in the ETP in association with abrupt thermoclines (Spear *et al.* 2001). Thus, lower abundance of the tuna-dependent species in La Niña years is not surprising because the thermocline is shallower and weaker during those conditions. Abundances of the petrel, shearwater, and tern were each highest in 1989, although that of the Red-footed Booby, more closely tied to breeding islands, showed somewhat different annual patterns.

Among the five tuna-independent species, the Tahiti Petrel was the only species having a significant annual trend – that of a decline (Figure 14). Because there were no trends observed among the other eight species/taxa we suspect that, rather than avoiding the study area, the decline was due to other factors, for example, a decline on the breeding colonies. The ETP is the most important part of this species' pelagic range where the great majority can be found at any given time. With the exception of the phalaropes, the highest abundance among tuna-independent species was observed in 1989 (similar to the pattern for three of the four tuna-dependent species). Thus, the only species showing different trends across years than that of the seven species having maximum abundance in 1989, were the phalaropes and Red-footed Booby, which both occur predominately along the coasts of the Americas (Figures 8 and 9). In that regard, both of these species had very similar annual trends, being most abundant in 1990 and 2000, and exhibiting much lower abundances in 1988, 1989, 1998, and 1999 (Figures 13 and 14).

**Figure 13.** Results of the GAMs analyses for population size and trends among the tuna-independent seabird species. Circles represent the point estimates for each year, vertical bars show the 95% confidence intervals for the point estimates, the horizontal line shows the smoothed trend calculated during the final GAM across years, and the dashed horizontal line shows the smoothed 95% confidence intervals estimated during the trends analysis.



**Figure 14.** Results of the GAMs analyses for population size and trends among the tuna-dependent seabird species. Circles represent the point estimates for each year, vertical bars show the 95% confidence intervals for the point estimates, the horizontal line shows the smoothed trend calculated during the final GAM across years, and the dashed horizontal line shows the smoothed 95% confidence intervals estimated during the trends analysis. The flat lines represent a no-trend result for each species.



### III. HABITAT RELATIONSHIPS

#### *Analyses*

Rather than to explicitly identify species-specific habitat preferences, our goal here was to investigate temporal patterns in relationships between seabird density and oceanic habitat. This approach is valuable because it allows for investigations of seabird responses to potential ecosystem changes in a way that investigations of distribution and abundance alone are not able to address. Species-specific habitat preferences should remain largely the same through time unless available habitat changes in some way, either through a change in the physical environment, or a change in the biological one (for example, through removal of a competitor, thereby allowing expansion into a previously occupied habitat). These types of ecosystem changes, while possibly resulting in changes in distribution and abundance, should be reflected in changes in habitat relationships.

Relationships between seabird density and oceanic habitat were quantified using Canonical Correspondence Analysis (CCA, ter Braak 1986) and implemented by the program CANOCO 4 (ter Braak and Šmilauer 1998). CCA is a multivariate method of analysis which relates two independent sets of variables (here, species and environmental). Specifically, it relates community composition to variation in the environment by choosing ordination axes from species data which are linear combinations of environmental variables. The method assumes that response surfaces of species to environmental gradients are uni-modal, not linear, and that sampling includes the entire range of each variable so as to completely sample a species' range of response. CCA is relatively robust to these assumptions, and is particularly appropriate for data sets containing many zero values, a feature typical of species abundance data sets, including the present data on seabird density.

Results of CCA can be used to identify habitat types from integrated combinations of individual habitat variables, to identify species-specific habitat preferences, and to identify relative similarity between species with respect to these preferences. Here we use CCA to investigate temporal patterns in these three measures by comparing time series of ordination results performed with data from single years, and by integrating data from all years into a single ordination (see below).

To quantify oceanic habitat, we chose a suite of seven oceanographic variables: sea surface temperature, sea surface salinity, surface chlorophyll concentration, sigma-t (an index of water density based on temperature and salinity), thermocline depth (the depth of maximum temperature gradient, calculated with an algorithm that ensured the temperature gradient extended through multiple data points), thermocline strength (the value of the maximum temperature gradient), and mean concentration of chlorophyll in the euphotic zone (the integrated chlorophyll concentration from the surface to the euphotic zone depth, estimated as in Morel 1988). We added two geographic variables to this set, latitude and longitude, for a total of 9 habitat variables. Previous studies of ETP seabirds have shown that these variables are important in understanding distribution and abundance (Ballance *et al.* 1997, Spear *et al.* 2001).

We calculated daily means for each oceanographic variable, and used these values with ship position at noon (latitude and longitude) to represent habitat sampled during each survey day. Surface and mean euphotic zone chlorophyll concentration values were log-transformed and all oceanographic and geographic variables were standardized to zero mean and unit variance to remove effects from differing scales of measurement. Daily seabird density values were standardized to birds recorded per 100 km<sup>2</sup> per day.

Each CCA was run using biplot scaling of interspecies differences (where species scores are the weighted averages of sample scores) so that each species' point in resulting ordination diagrams (see Figure 25) is at the center of its niche and represents most accurately the dissimilarities between the occurrence patterns of different species. Species data were not transformed prior to analysis, although rare species were down-weighted. The result of these treatments is that extreme density values for a given species will tend to have relatively high influence on the ordination results, but the influence of rare species on the ordination will not be large relative to abundant species.

In order to investigate effects of interannual variation, we added 8 additional categorical variables, six representing each survey year, and two representing each survey decade (MOPS and STAR). The significance of this variation was judged as in Reilly and Fiedler (1994) by first performing the CCA using oceanographic and geographic variables only, then again adding year/decade variables to investigate the additional contribution to variance explained (see below).

### *Results and Discussion - Years Analyzed Separately*

The following results pertain to yearly ordinations performed with the seven oceanographic and two geographic variables included as measures of oceanic habitat.

Nine indicator species. The first four canonical axes explained between 25.8 and 39.1 percent of the variance in species density, depending upon year (Table 4). This variance was largely accounted for by the first and second axes, with the first explaining approximately twice the amount of the second. Therefore, we confine subsequent investigations to these first two axes only. There were some exceptions to this pattern; in 1990 the first two axes explained almost equal proportions of variance, and in 2000 the third axis explained almost as much as the second. There is some interannual variation with respect to explained variance for each axis, and for the total.

The fact that the amount of variance in seabird density explained by these ordinations is not higher is partly (perhaps largely) explained by the fact that our data contain birds that are not only using the habitat in which we recorded them (*i.e.* feeding), they also contain birds that are simply commuting through it. These commuting birds may not have selected the habitat over which they were recorded; this likely introduces a fair bit of noise in the data set.

**Table 4.** Ordination results from canonical correspondence analyses (CCA) of seabird density and oceanic habitat as defined by seven oceanographic and two geographic variables. Each CCA was run with nine indicator species and data from one year only. Values represent percent of variance in seabird density explained by each of the first four canonical axes. “Total” is cumulative percent variance in seabird density explained by first four axes.

	----- Canonical Axes -----				
	1	2	3	4	Total
<b>1988</b>	16.3	9.4	3.8	3.0	32.5
<b>1989</b>	18.0	9.7	3.8	1.7	33.2
<b>1990</b>	11.6	10.3	2.4	1.5	25.8
<b>1998</b>	19.6	4.7	4.3	2.7	31.3
<b>1999</b>	14.4	7.8	2.5	2.4	27.1
<b>2000</b>	19.7	8.7	7.4	3.3	39.1

The relationships between each species/taxon and habitat identified by the first two canonical axes were for the most part unimodal (Appendix 1). Thus a primary assumption of CCA was satisfied.

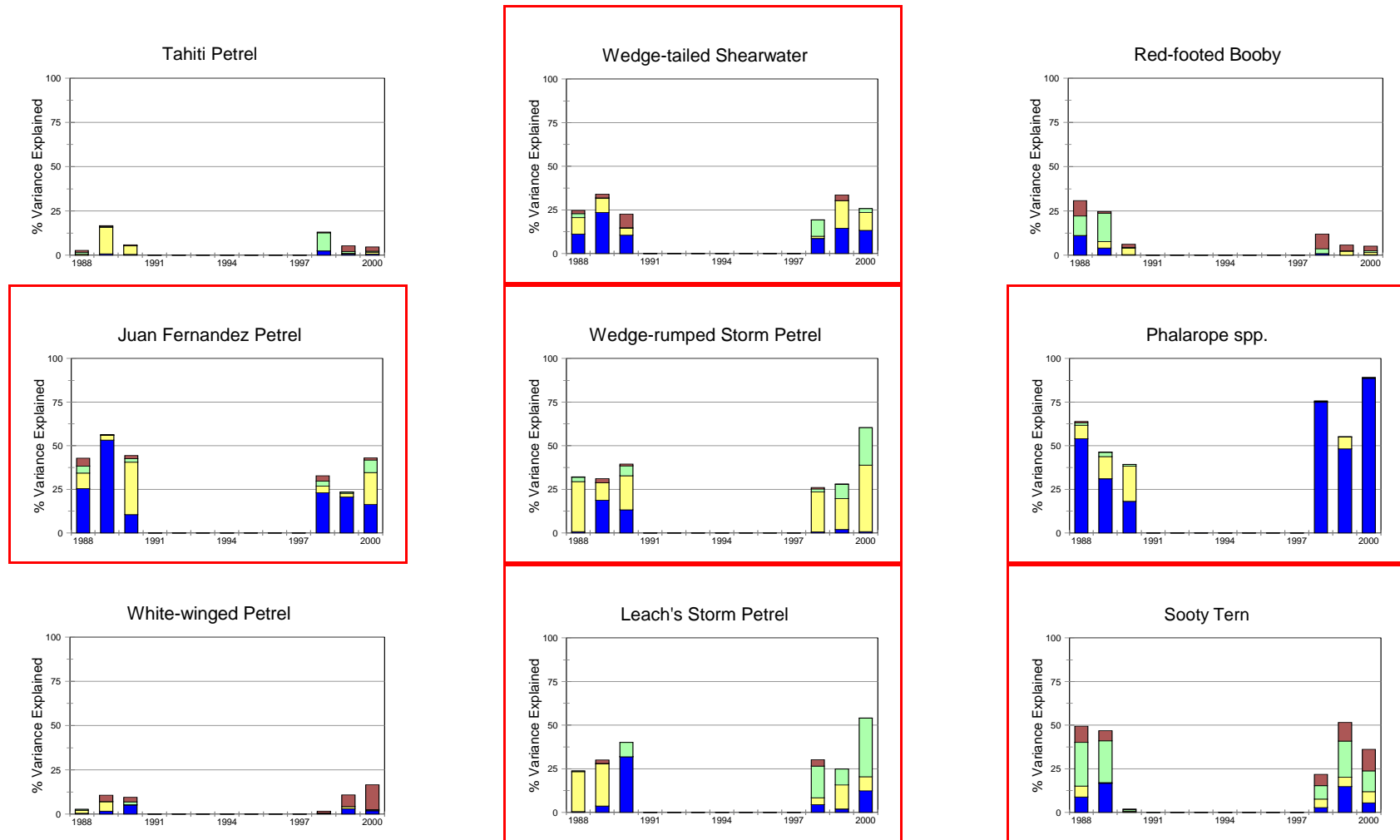
The explanatory power of the CCA varied with species. This is shown by Figure 15, which illustrates the following three patterns.

First, the ordinations explain a high proportion of variation in density for some species and little for others. In the former category are phalaropes, where greater than 50% of variance was explained by the first four axes in four of the six years, and Juan Fernandez Petrel, Wedge-tailed Shearwater, Wedge-rumped and Leach’s Storm-petrels, and Sooty Tern, for which greater than 25% of variance was explained in most years. The ordinations explained much less of the variance in density for Tahiti and White-winged petrel, and Red-footed Booby. Therefore, interpretations of ordination patterns will focus on those species in the former category, less on those in the latter.

Second, there are distinct species-specific patterns with respect to which axes explain the greatest proportion of variance. Most notably, axis 1 explains a high proportion of variance for phalaropes and, to a lesser extent, Juan Fernandez Petrels and Wedge-tailed Shearwaters. But for Wedge-rumped Storm-petrel, axis 2 is more important, whereas for Sooty Tern, axis 3 explains the greatest amount of its variance in density. Investigations of species-specific patterns will therefore focus on the relevant axis, which will not necessarily be axis 1.

Third, whereas the above two patterns are broadly consistent over most years, there is some interannual variation with respect to the proportion of variance explained by the ordination, and the relative contributions of the first four axes to the total variance explained.

**Figure 15.** Temporal patterns in percent variance in a given species' density explained by each of the first four canonical axes: Blue = Axis 1; Yellow = Axis 2; Green = Axis 3; Brown = Axis 4, and all axes together (total bar height). The ordination explains 25% or more of the variance in density for most years for the six species outlined in red.



With respect to the scale of the entire study (all years), axis 1 defined the same general habitat type over time. This can be seen in Figure 16, where it is clear that the sign of scores for the 9 habitat variables on the first canonical axis is generally the same across all years. Scores are correlation coefficients when data are standardized, so that the magnitude of scores can be used as an indication of the importance of a particular environmental variable. Thus, axis 1 generally defines habitat with cool surface water, high chlorophyll content, and a shallow and weak thermocline, generally near the eastern section of the study area. On a shorter temporal scale, some interannual variation with respect to the contribution of each variable to this habitat type can be seen.

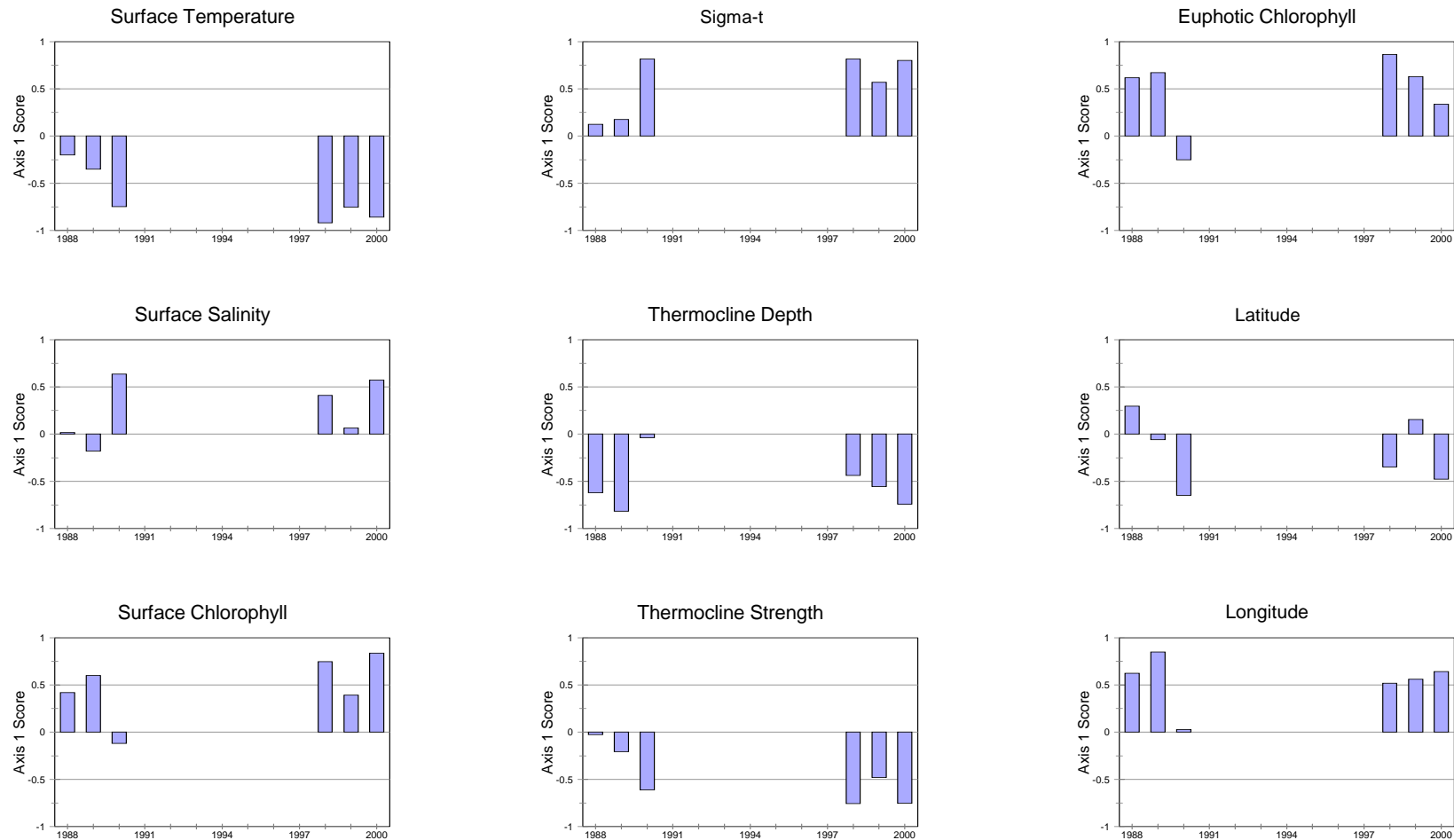
The same patterns apply to habitat defined by axis 2 (Figure 17). Over the entire study period, axis 2 generally defines the same habitat (cool, high-density surface water with shallow, weak thermoclines in southern latitudes toward the east of the study area). Some interannual variation with respect to the contribution of each variable to this habitat is also apparent.

The first canonical axis was important in explaining variance for phalaropes, Juan Fernandez Petrels, and Wedge-tailed Shearwaters; less so for others (Figure 15). For these three species, the response to this habitat showed broadly similar patterns over time. Phalaropes associated with it (with the notable exception of 1990), and Juan Fernandez Petrels and Wedge-tailed Shearwaters avoided it (Figure 18). Notable here is the fact that tuna-dependent and tuna-independent species showed habitat associations that reflected their guild membership. Specifically, tuna-dependent species (Juan Fernandez Petrels and Wedge-tailed Shearwaters) avoided this habitat and tuna-independent species (phalaropes) associated with it.

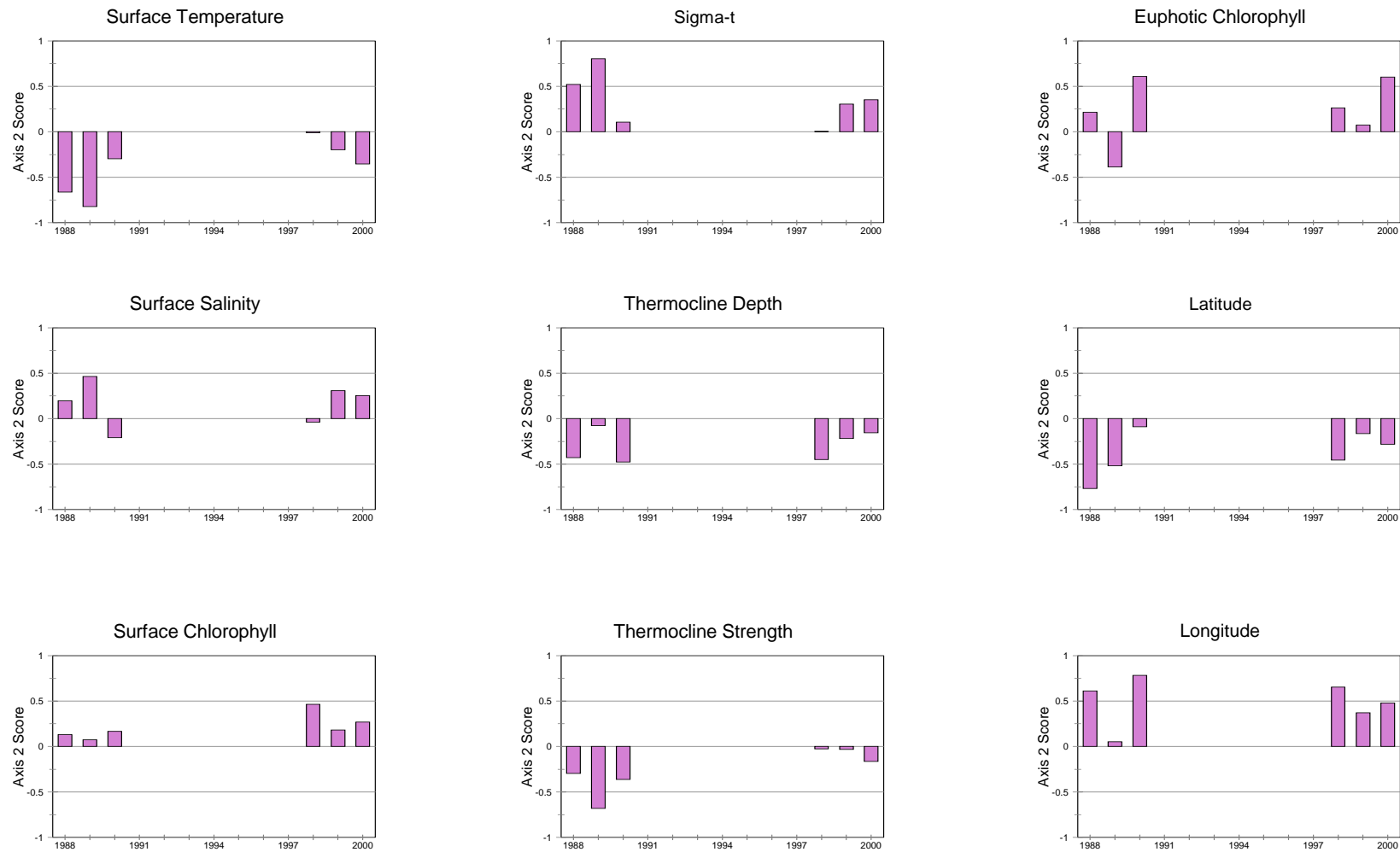
The second canonical axis was important in explaining variance for Wedge-rumped Storm-petrels; less so for other species (Figure 15). Across all years, this species associated with habitat identified by axis 2 (Figure 19).

In summary: a) axes 1 and 2 were most informative, explaining between 20 and 30% of the variance in species density; b) the habitat identified by axis 1 was generally the same across time, though there was some interannual variation with respect to the degree of contribution from specific oceanographic and geographic variables to this habitat type; c) patterns for axis 2 were similar (*i.e.* the habitat type was generally consistent across time with some interannual variation in degree of contribution from certain variables evident); d) for those species for which CCA explains a relatively high amount of variance, habitat association patterns were relatively consistent across time; e) tuna-dependent and tuna-independent species showed habitat associations that reflected their guild membership; these associations remained broadly consistent over time.

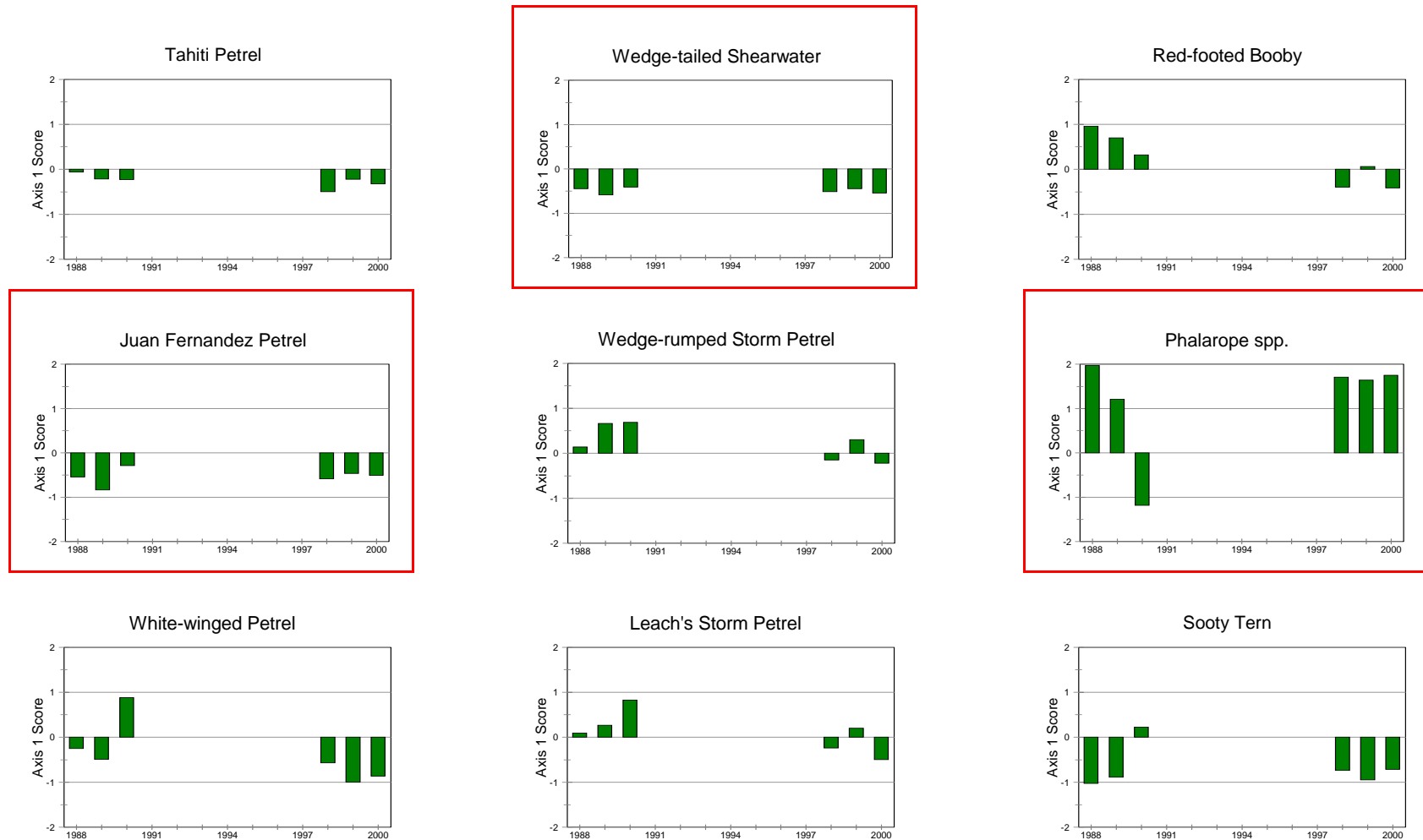
**Figure 16.** Scores of 7 oceanographic and 2 geographic habitat variables on canonical axis 1, by year. This axis explains between 11.6 (1990) and 19.7% (2000) of the variance in overall species density (nine species used in the ordination), depending upon year. The plots show that axis 1 broadly defines habitat with cool surface water, high chlorophyll content, shallow and weak thermoclines, generally near the eastern section of the study area. Some interannual variation can be seen.



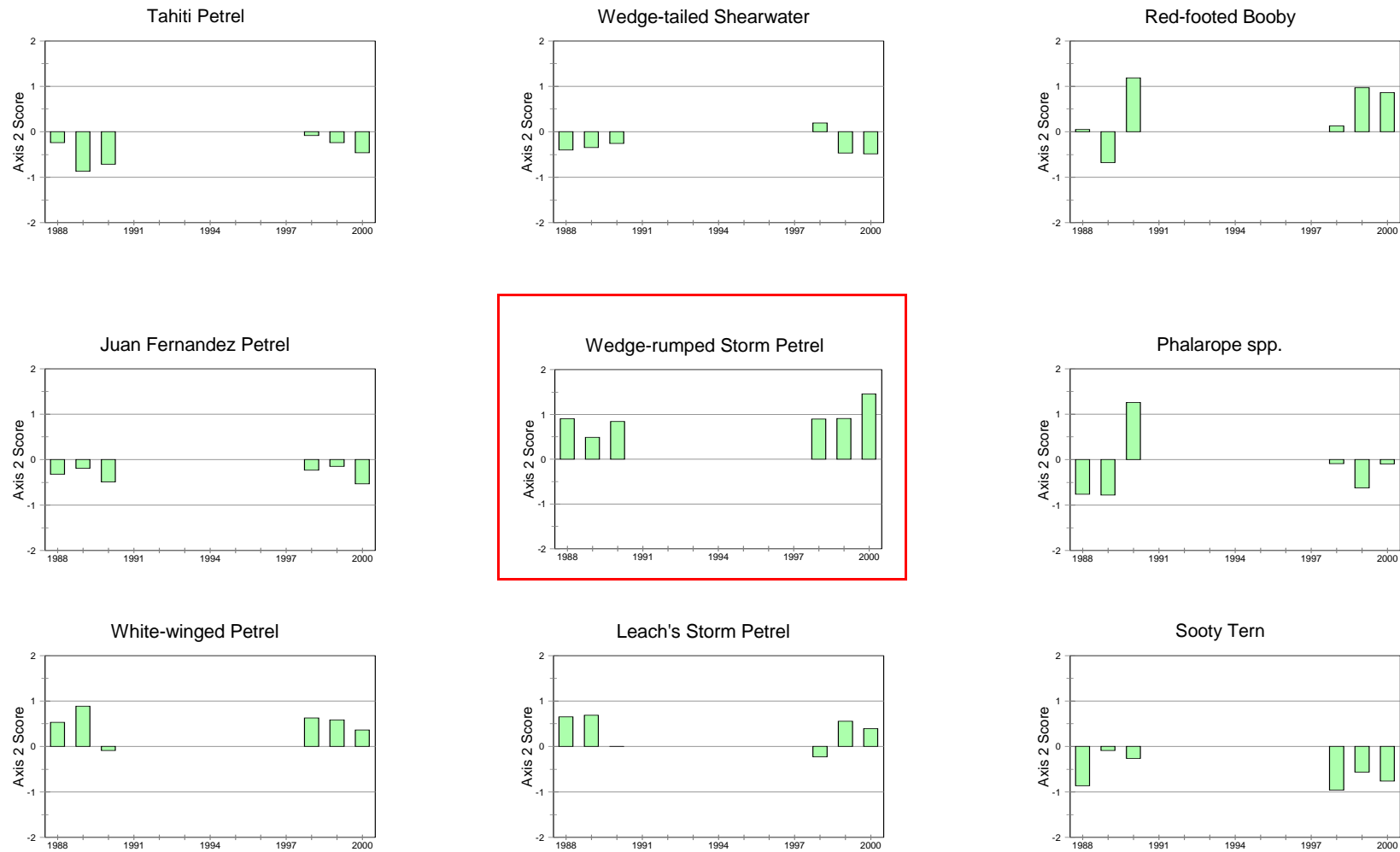
**Figure 17.** Scores of 7 oceanographic and 2 geographic habitat variables on canonical axis 2, by year. This axis explains between 4.7 (1998) and 10.3% (1990) of the variance in species density (nine species used in the ordination), depending upon year. Axis 2 broadly defines cool, high-density surface water with shallow, weak thermoclines in southern latitudes toward the east of the study area.



**Figure 18.** Scores of 9 seabird species/taxa on canonical axis 1, by year. This axis is important in explaining variance for phalaropes, Juan Fernandez Petrels, and Wedge-tailed Shearwaters (outlined here with red boxes; see Figure 15) and broadly defines habitat with which the former associates and the latter two avoid. Association patterns are largely consistent over time with the exception of phalaropes in 1990.



**Figure 19.** Scores of 9 seabird species/taxa on canonical axis 2, by year. This axis is important in explaining variance for Wedge-rumped Storm-petrels (outlined here with red; see Figure 15). Habitat association patterns are largely similar across time, though some interannual variation is evident.



Eight Indicator Species. The ordinations described in the previous section were heavily influenced by phalaropes. Because the focus of the IDCPA investigations center on the oceanic ecosystem, and because phalaropes are predominantly coastal migrants (Table 1 and Figure 9), we removed this taxa from the data and performed a second series of ordinations using the remaining eight species.

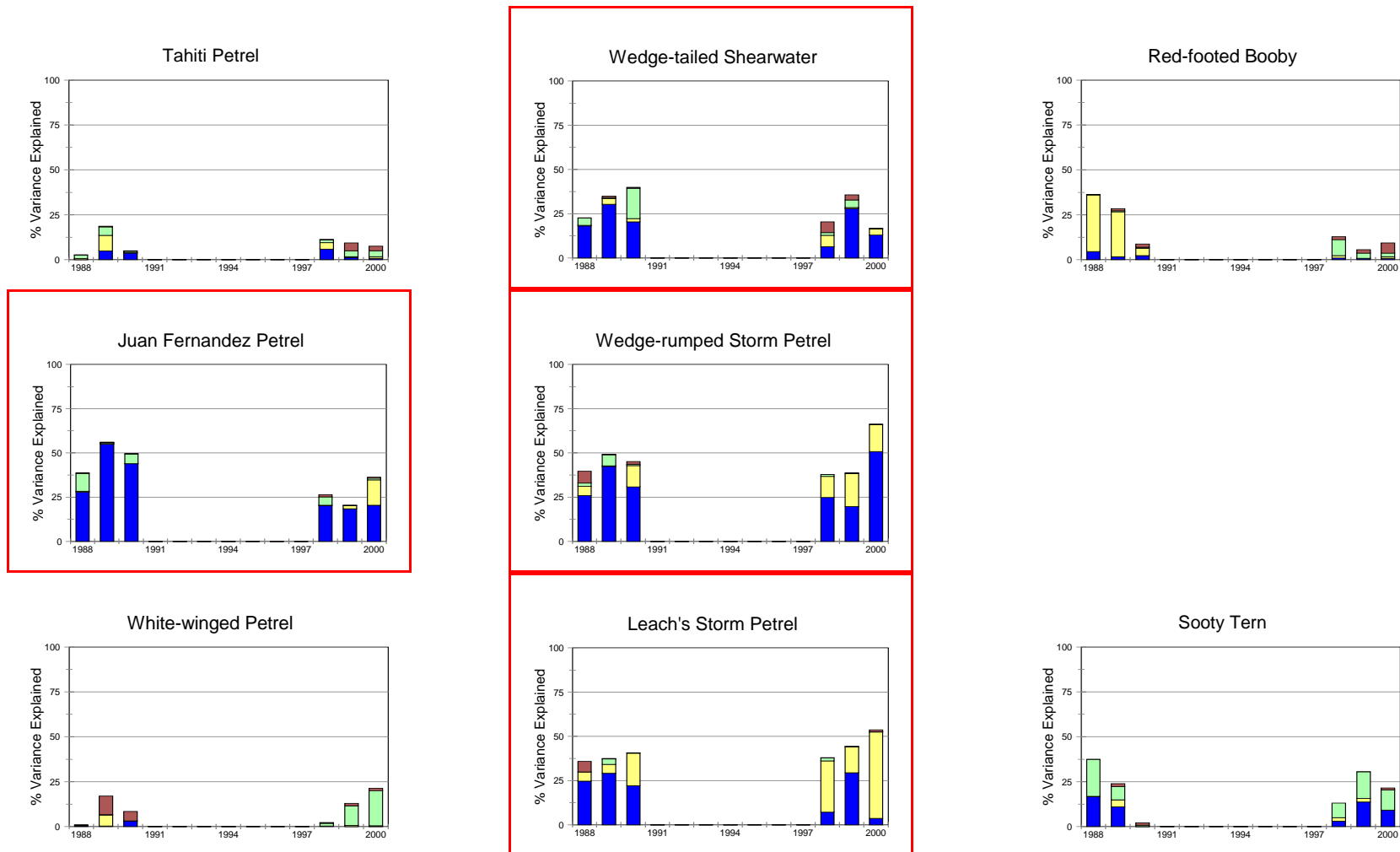
This new series of ordinations explained between 21.7 and 33.8 percent of the variance in species density (first four axes only, Table 5). As was the case with the nine-species ordinations, variance was largely accounted for by the first and second axes, and again, subsequent investigations will be confined to these. (The relationship between each species and habitat identified by these first two axes was generally unimodal as illustrated in Appendix 2.) Also similar to the ordinations performed with nine species, there is some interannual variation with respect to the amount of variance explained by each axis, and by all axes.

**Table 5.** Ordination results from canonical correspondence analyses (CCA) of seabird density and oceanic habitat as defined by seven oceanographic and two geographic variables. Each CCA was run with eight indicator species and data from one year only. Values represent percent of variance in seabird density explained by each of the first four canonical axes. “Total” is cumulative percent variance in seabird density explained by first four axes.

	----- Canonical Axes -----				Total
	1	2	3	4	
<b>1988</b>	13.8	8.9	4.2	1.6	28.5
<b>1989</b>	20.6	8.6	2.7	1.9	33.8
<b>1990</b>	15.5	5.9	2.3	1.6	25.3
<b>1998</b>	9.2	7.2	4.1	1.2	21.7
<b>1999</b>	14.0	6.2	3.8	1.1	25.1
<b>2000</b>	11.9	10.4	4.7	2.0	29.0

The ordinations explained 25% or more of the variance in species density for most years for four species: Juan Fernandez Petrels, Wedge-tailed Shearwaters, and Wedge-rumped and Leach’s storm-petrels (Figure 20). For all of these, the first axis was most important, although axis 2 was important to Leach’s Storm-petrels in 1998 and 2000. And, as was the case with the nine-species ordinations, there was some interannual variation with respect to the proportion of variance explained, and the relative contributions of the first four axes to the total variance explained.

**Figure 20.** Temporal patterns in percent variance in a given species' density explained by each of the first four canonical axes: Blue = Axis 1; Yellow = Axis 2; Green = Axis 3; Brown = Axis 4, and all axes together (total bar height). The ordinations explain 25% or more variance for most years for four species: Juan Fernandez Petrels, Wedge-tailed Shearwaters, and Wedge-rumped and Leach's storm-petrels (outlined below with red boxes).



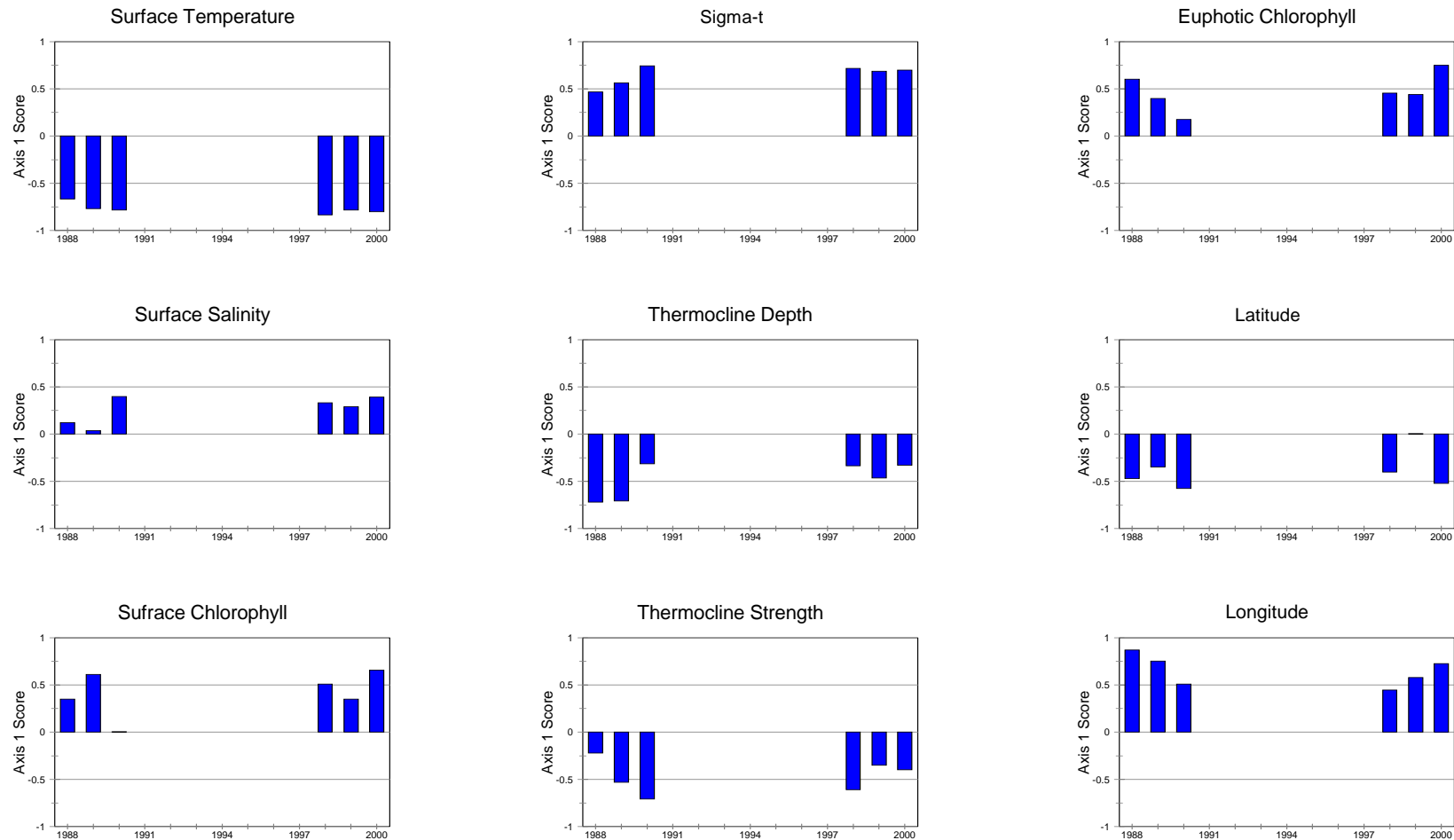
Temporal patterns in habitat identified by each axis, and in species association with this habitat were similar to those for the nine-species ordinations described earlier. The following three points summarize these results.

First, with no exceptions, the sign of the score for each of the nine habitat variables with respect to the first canonical axis was the same across all years. This axis generally defined cool, dense surface water with high chlorophyll content, and shallow and weak thermoclines, near the southern and eastern sections of the study area, although the contribution of each variable to this axis varied interannually (Figure 21).

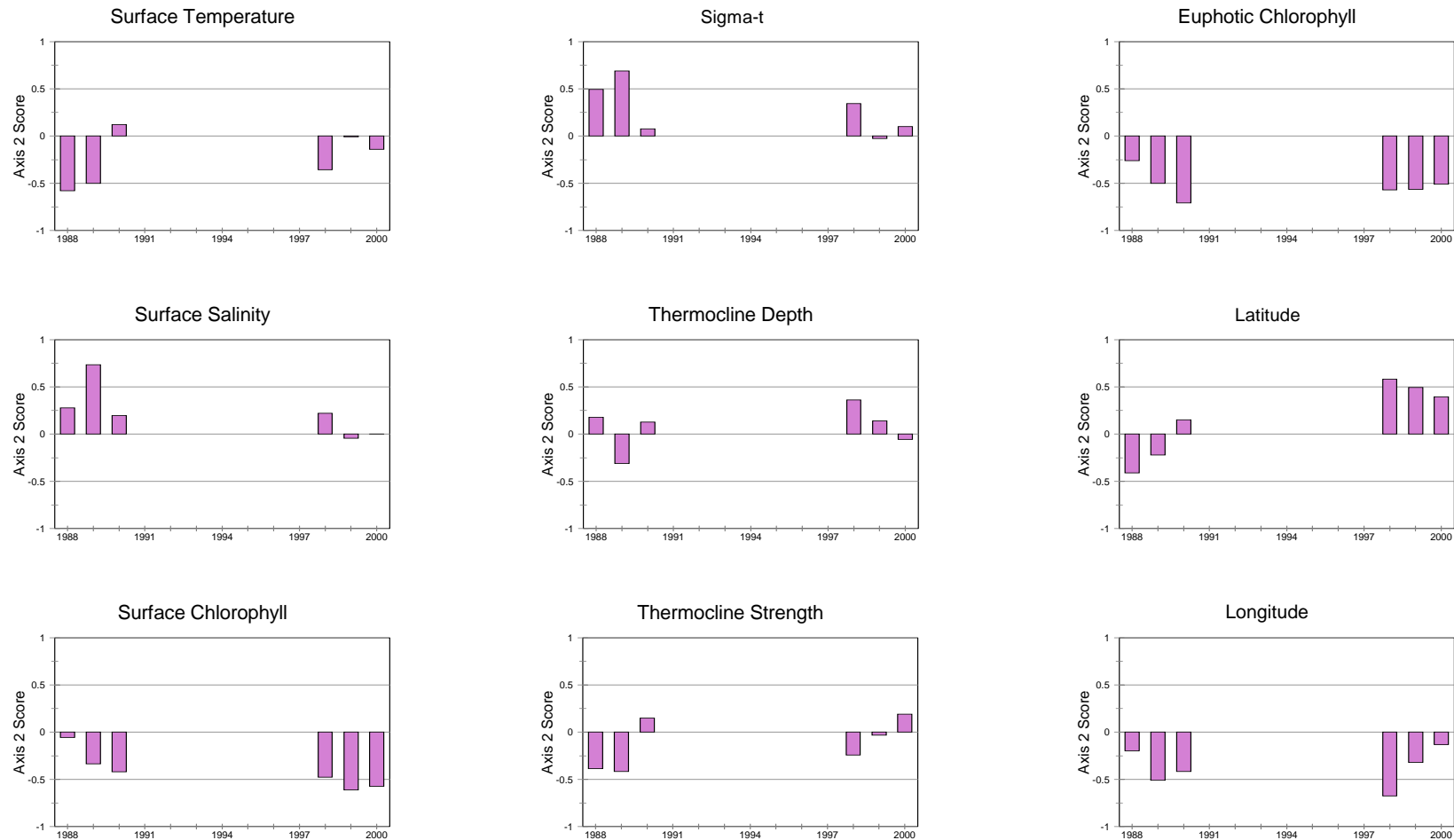
Second, axis 2 generally defined similar habitat across all years, though the degree of interannual variation was greater than for axis 1 (Figure 22). This habitat defined waters low in chlorophyll with high density near the western part of the study area.

Third, for those species for which CCA explained a relatively high proportion of variance, habitat associations were relatively consistent across time. Axis 1, important to four species, defined habitat which two avoided in all years (Juan Fernandez Petrels and Wedge-tailed Shearwaters), and with which two associated in all years (Wedge-rumped and Leach's storm-petrels; Figure 23). Axis 2, important to Leach's Storm-petrel, defined habitat with which it invariably associated (Figure 24).

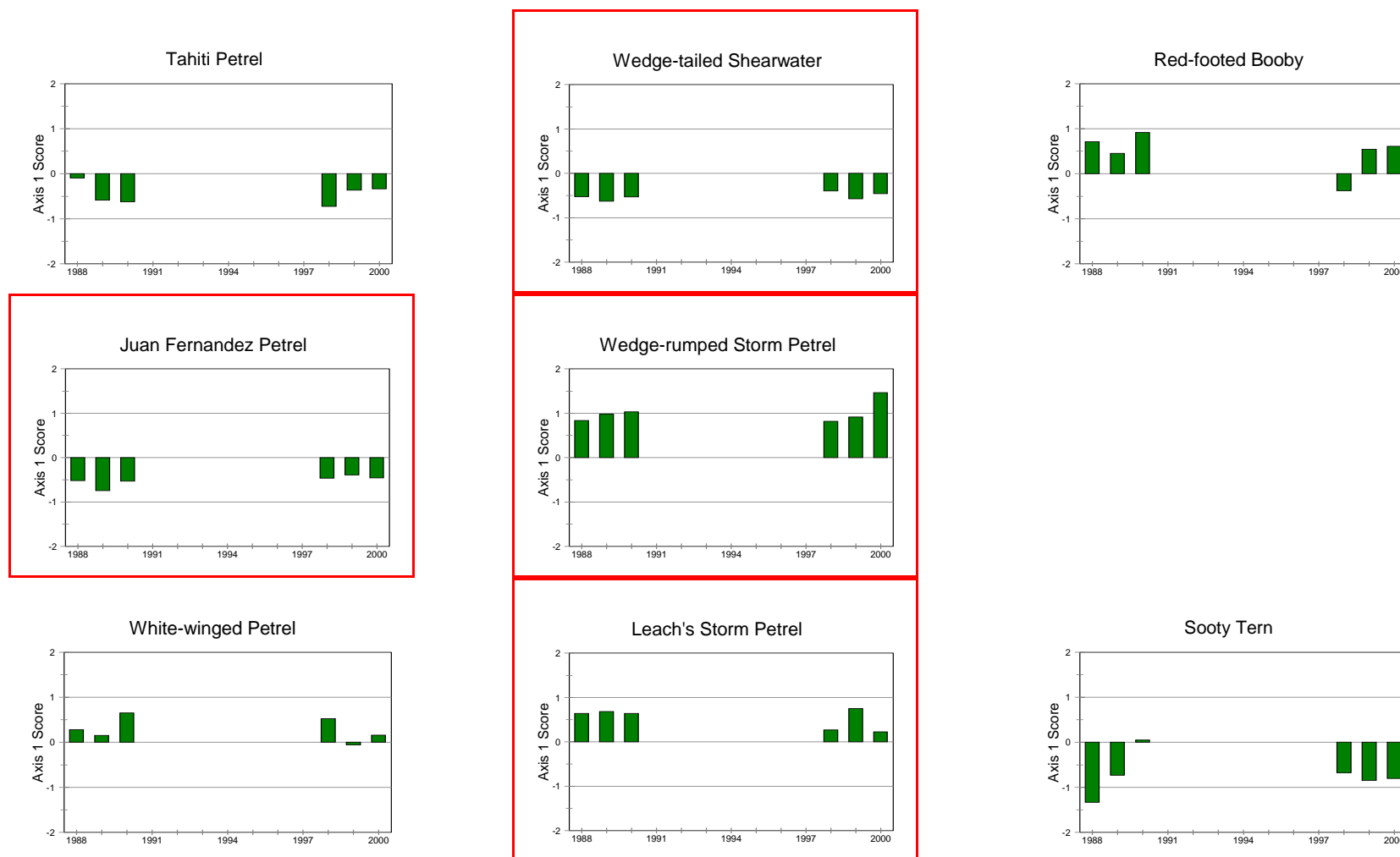
**Figure 21.** Scores of 7 oceanographic and 2 geographic habitat variables on canonical axis 1, by year. This axis explains between 9.2 (1998) and 20.6% (1989) of the variance in overall species density (eight species included in ordinations), depending upon year. The plots show that axis 1 broadly defines habitat with cool, dense surface water, high chlorophyll content, shallow and weak thermoclines, generally near the eastern section of the study area. Some interannual variation can be seen.



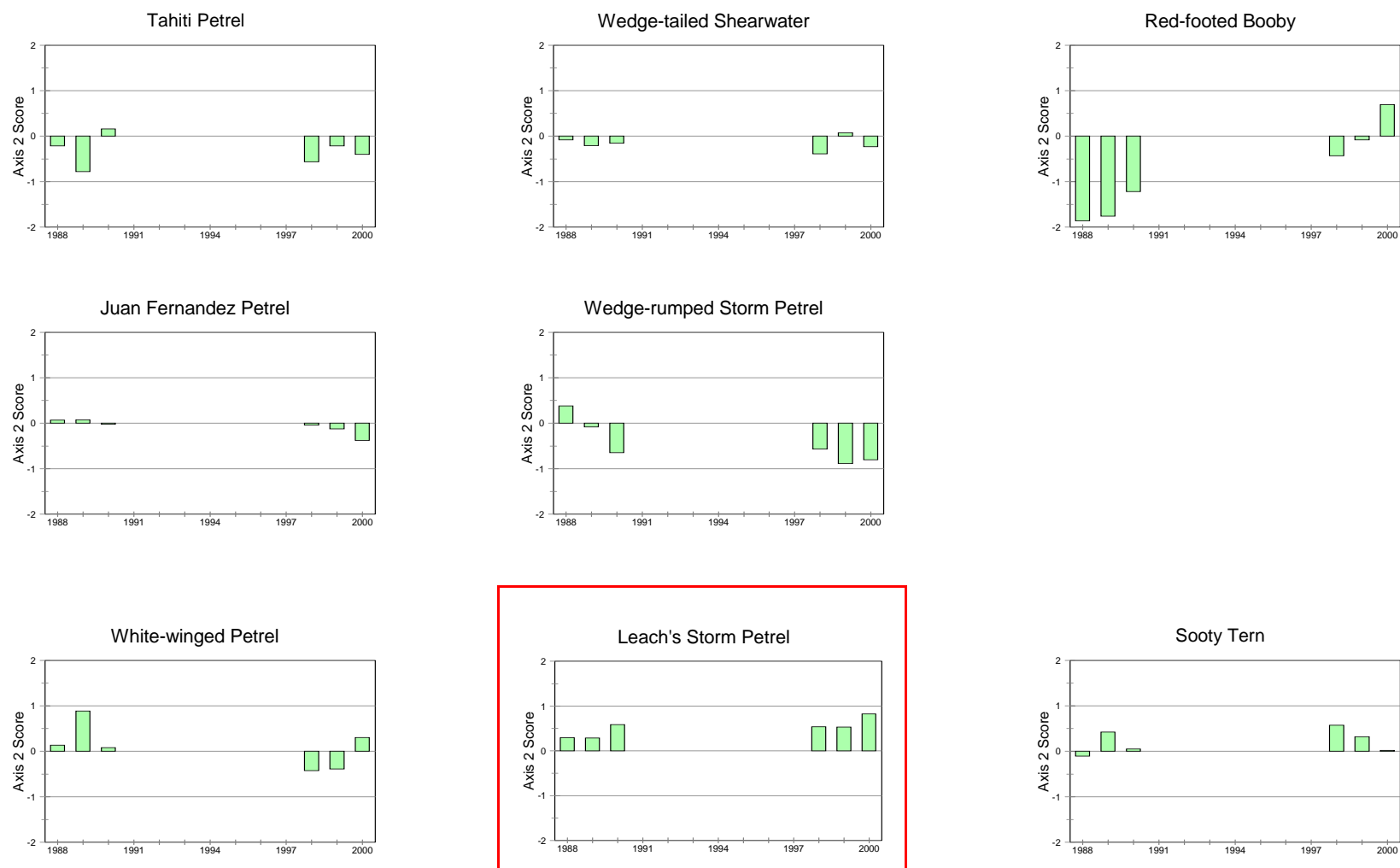
**Figure 22.** Scores of 7 oceanographic and 2 geographic habitat variables on canonical axis 2, by year. This axis explains between 5.9 (1990) and 10.4% (2000) of the variance in species density (eight species included in ordinations), depending upon year, and generally defines waters low in chlorophyll with high density near the western part of the study area. Some interannual variation can be seen.



**Figure 23.** Scores of 8 seabird species on canonical axis 1, by year. This axis is important in explaining variance for Juan Fernandez Petrel, Wedge-tailed Shearwater, Wedge-rumped Storm-petrel, and, to a lesser extent, Leach's Storm-petrel (outlined here with red boxes; see Figure 20). It broadly defined habitat which the first two avoid, and with which the second two associate.



**Figure 24.** Scores of 8 seabird species on canonical axis 2, by year. This axis is important in explaining variance for Leach's Storm-petrel (outlined here with red; see Figure 20) and defines habitat with which it invariably associated.



## Results and Discussion - All Years Combined

The following results pertain to ordinations performed with data from all years analyzed together using different sets of variables to represent habitat sampled. These sets are oceanographic, geographic, year, and decade variables.

Relative to all four types of variables, oceanographic and geographic variables explained the highest proportion of variance in species data (Table 6). This was the case for ordinations performed with both nine and eight species (18.9% and 19.4% of variance explained, respectively). Year explained a higher proportion of variance than decade, adding approximately 1% to the total variance explained (year variables added to oceanographic and geographic) as compared to a few tenths of a percent (decade variables added to oceanographic and geographic). And the use of year variables as the only environmental variables explained just over 1% of the variance in species data.

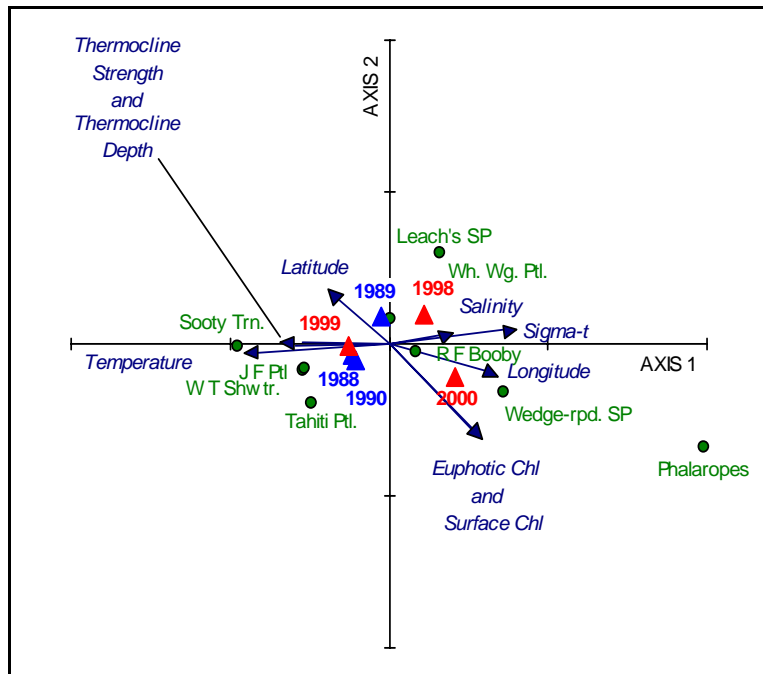
**Table 6.** Comparative ordinations from canonical correspondence analysis (CCA) of seabird density (nine indicator species included) and oceanic habitat as defined by oceanographic and geographic variables with different sets of interannual variables included. Each CCA was run with data from all years combined.

% Variance in Species Density Explained by First Four Axes	----- Habitat Variables Included in Analysis -----				
	Oceanographic and Geographic	Oceanographic, Geographic, and Year	Oceanographic, Geographic, and Decade	All Variables	Year Only
Nine Species Used in Ordination	18.9	20.0	19.2	20.0	1.8
Eight Species Used in Ordination	19.4	20.3	19.5	20.3	1.1

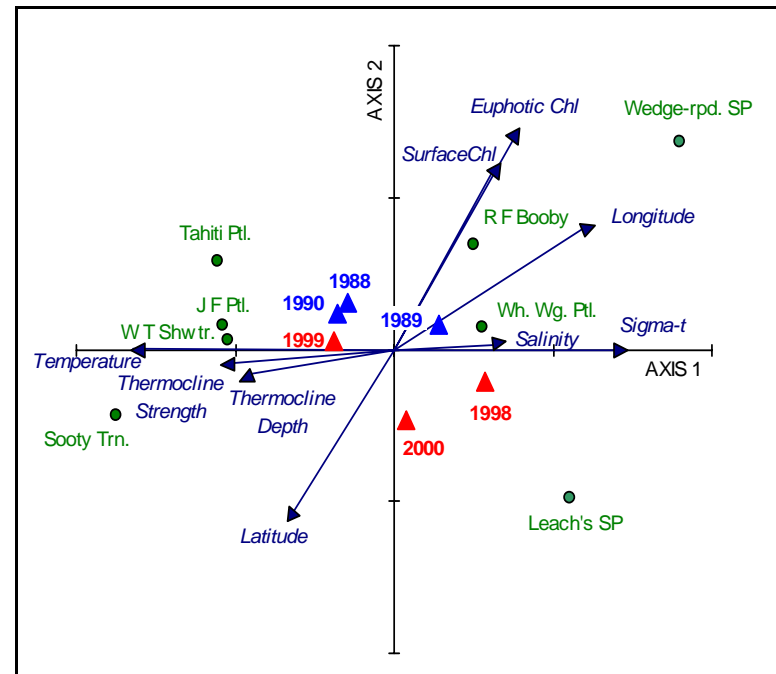
A final indication of the influence of temporal variation on the ordination can be seen with a biplot, typically used in CCA. Biplots illustrate the contribution of the environmental variables to the first two canonical axes, and species response to these same habitat axes. In the present case, the ordination of all years together results in a biplot representing an integrated mean of the influence of habitat variables on each canonical axis, and the relative location of each species with respect to these axes (Figure 25). The centroid points corresponding to each year have been added to the biplot. They clearly illustrate the interannual variation, but give no qualitative indication of any larger temporal scale trend, for both ordinations with nine (Figure 25A) and eight species (Figure 25B).

**Figure 25.** Ordination biplot from CCA using oceanographic, geographic, and year variables to explain species density. Data from all years were combined. The contribution of oceanographic and geographic variables to each canonical axis can be interpreted from the direction and length of the lines corresponding to each variable. The response by each species is indicated by the points, which represent the center of that species' niche with respect to the habitat axes. Centroid values for each year are plotted and color-coded according to decade: red = MOPS, blue = STAR. The biplot using nine (A) and eight species (B) qualitatively illustrate the same temporal patterns.

(A)



(B)



## CONCLUSIONS

In general, these analyses and results indicate species- and foraging guild-specific patterns that are broadly consistent over time, with variation between years qualitatively stronger than variation between decades. To summarize, species-specific distribution patterns were consistent across time on a large spatial scale, but interannual variation in these patterns on a finer spatial scale was evident. Abundance of individuals for a given species fluctuated with year, but with the exception of one species, there was no significant trend over the entire study period. Species showed specific habitat association patterns that remained consistent over time, with some interannual variation evident. Tuna-dependent and tuna-independent species showed habitat associations that reflected their guild membership; these associations also remained consistent over time.

These conclusions mirror those of Fiedler and Philbrick (2002) in that regional effects of El Niño and La Niña are clearly visible in the oceanography of the ETP, and appear to dominate any longer-term (*i.e.* decadal-scale) signals.

## ACKNOWLEDGMENTS

We sincerely thank the many seabird observers who collected data in the field, and the officers and crew of the research vessels *David Starr Jordan*, *McArthur*, and *Endeavor*. Jenna Borberg, Josh Fluty, Robert Holland, Kathy Hough, and Paula Olson provided invaluable assistance with data edit, processing, and figure preparation.

## LITERATURE CITED

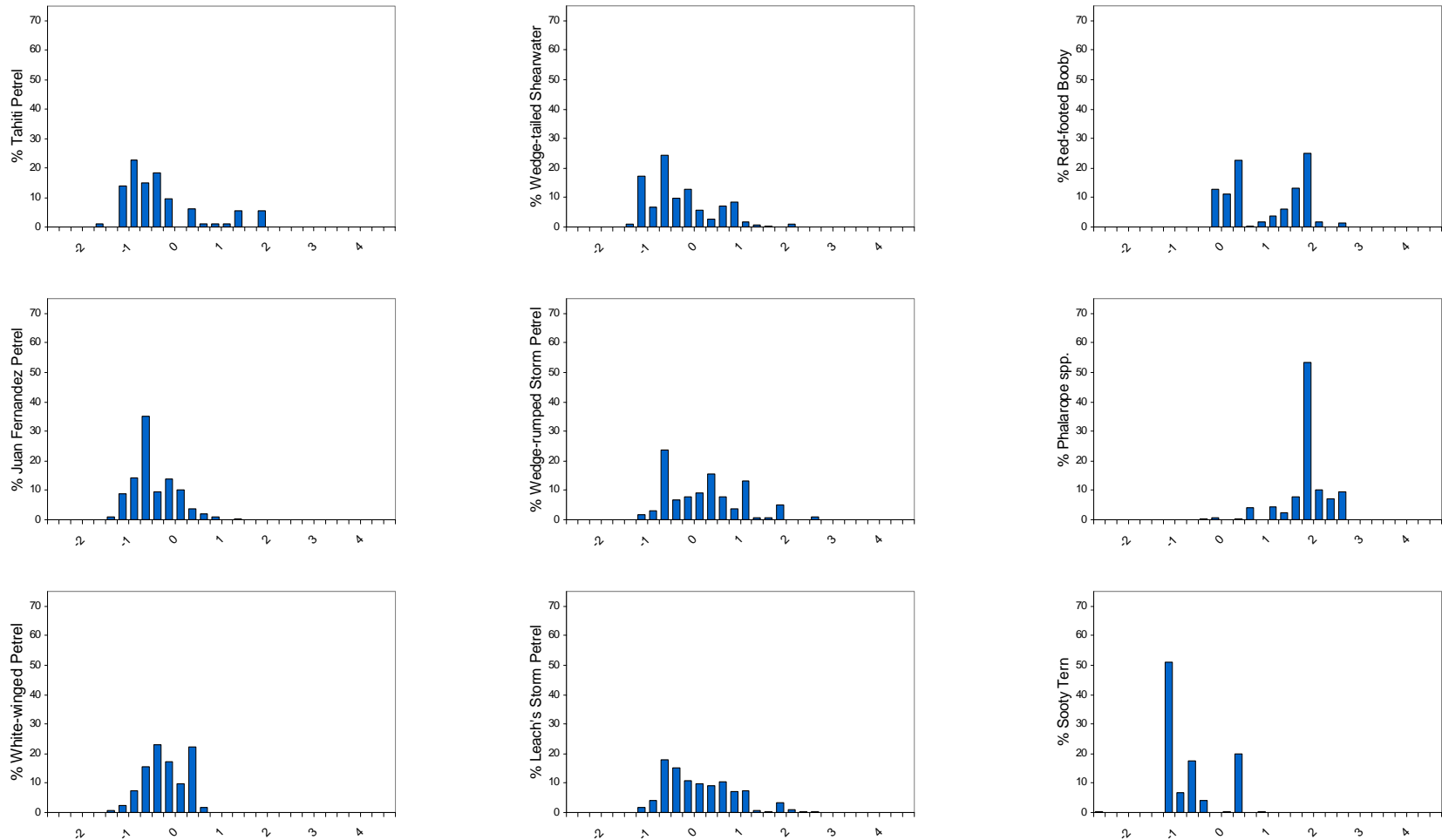
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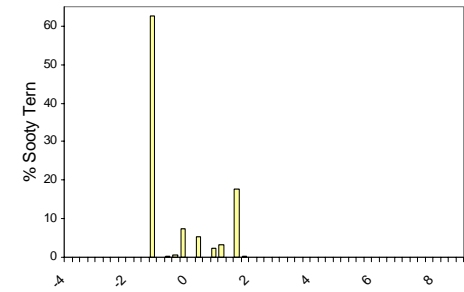
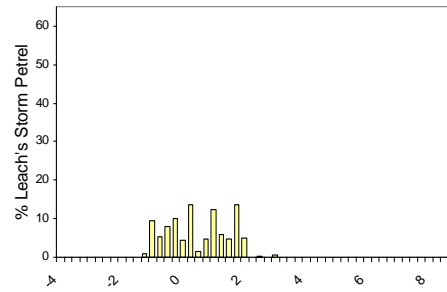
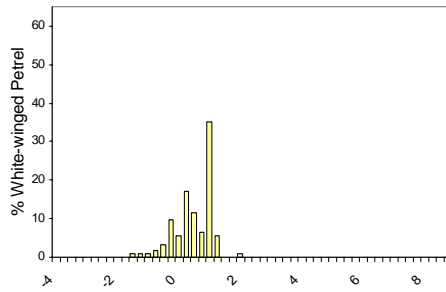
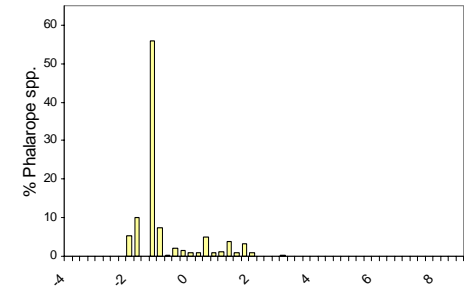
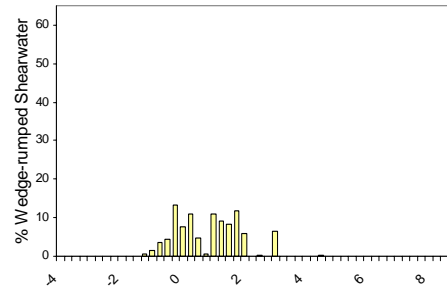
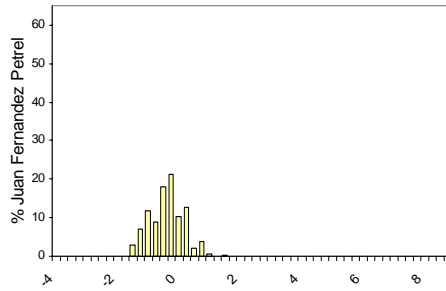
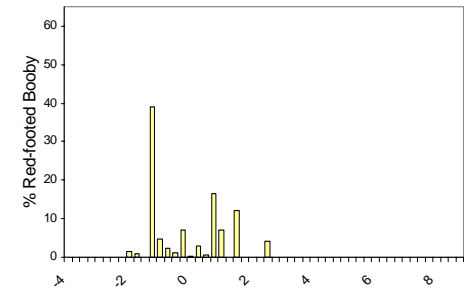
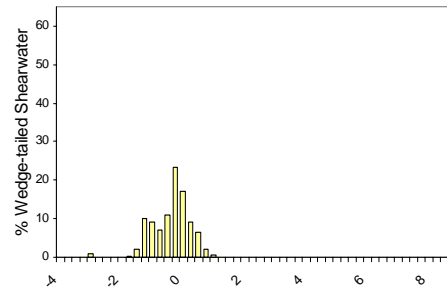
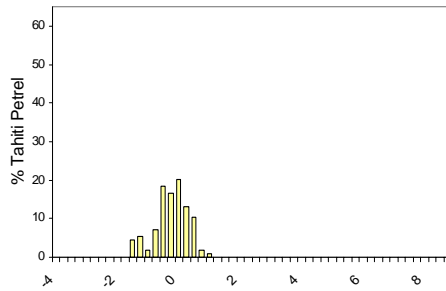
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**APPENDIX 1.** Frequency histograms (by year), transformed to percentages, of the first two environmental axis scores where each of nine seabirds were sighted. (Results from nine species used in the ordination). Relationships are for the most part unimodal, thus validating an assumption of CCA.

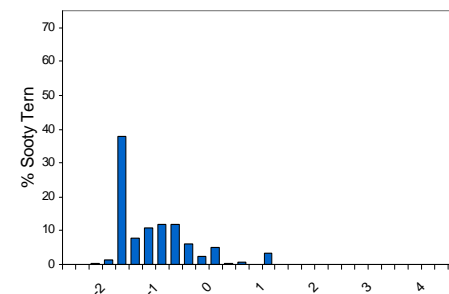
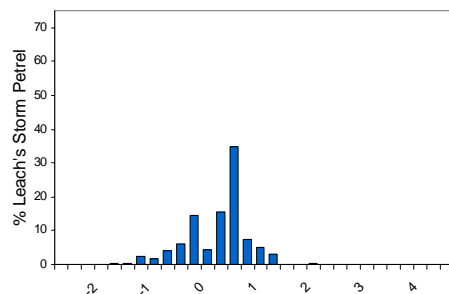
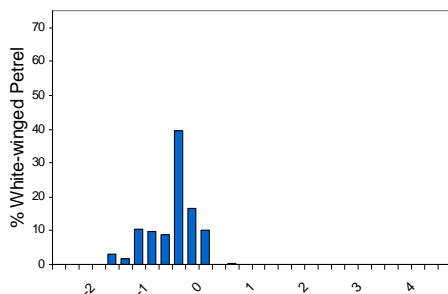
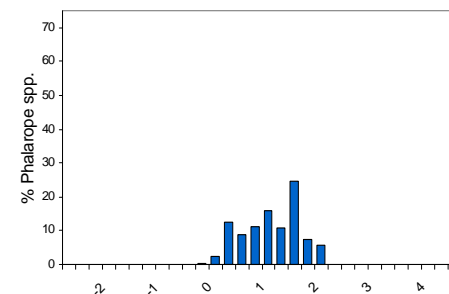
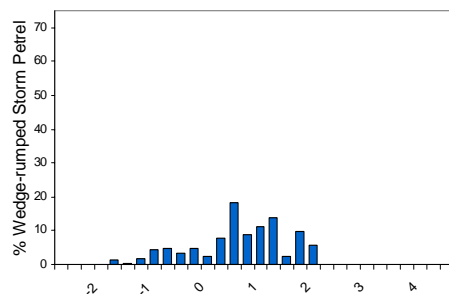
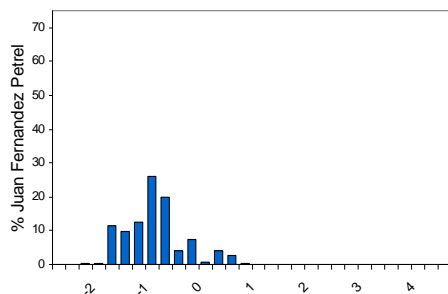
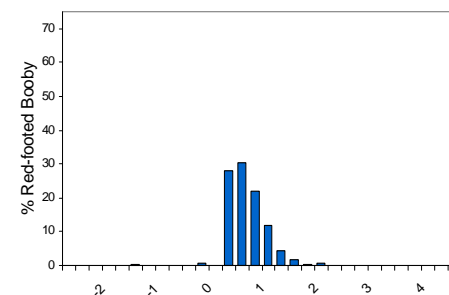
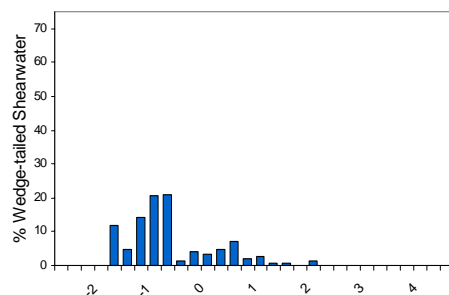
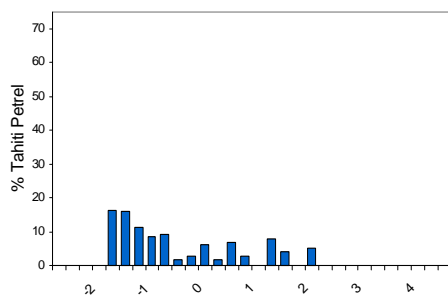
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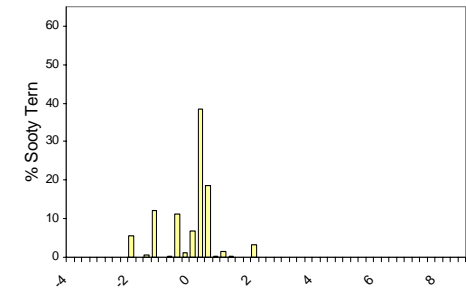
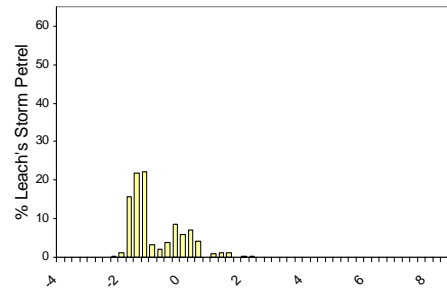
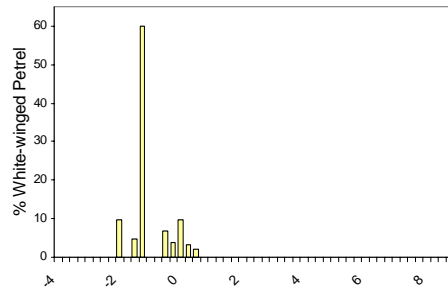
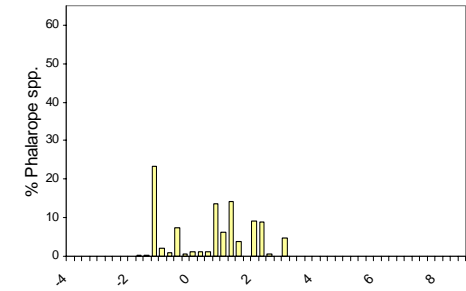
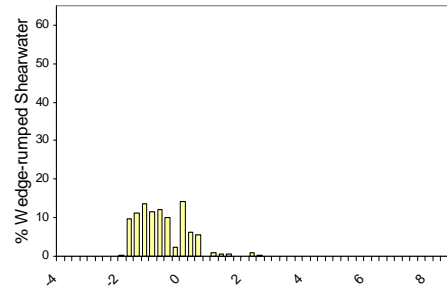
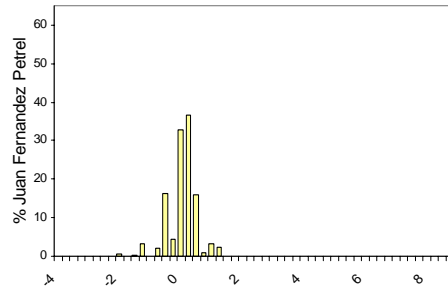
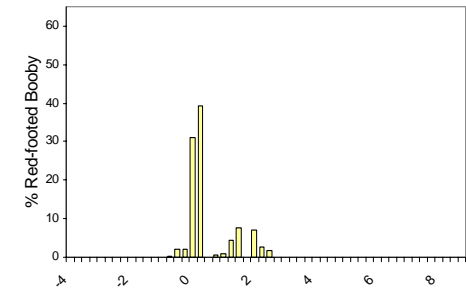
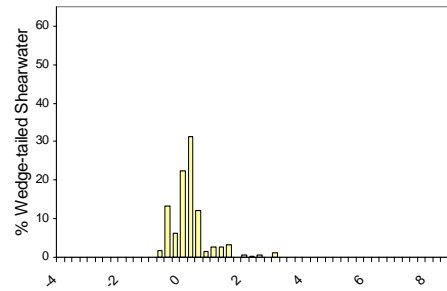
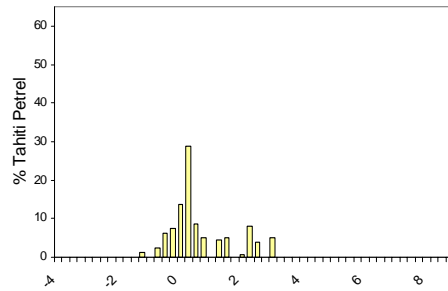
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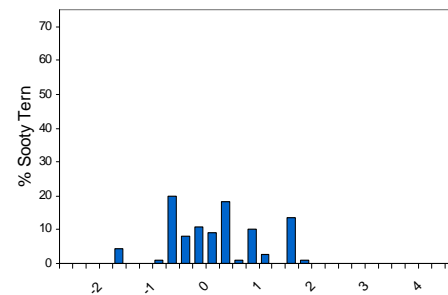
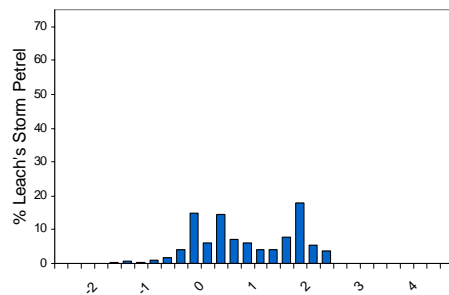
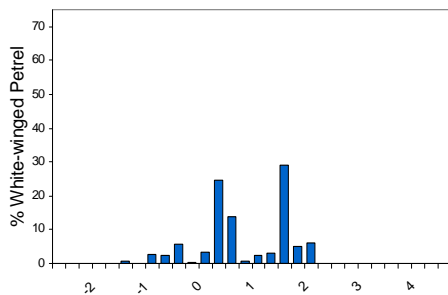
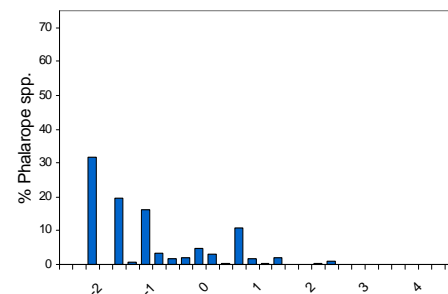
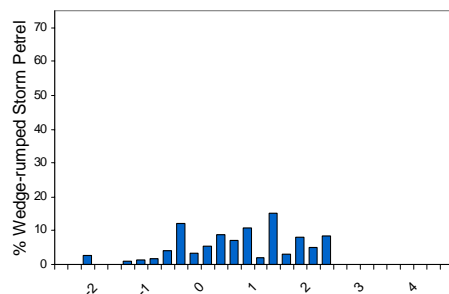
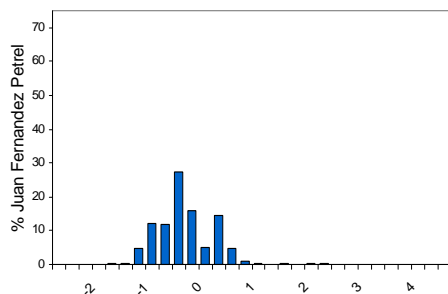
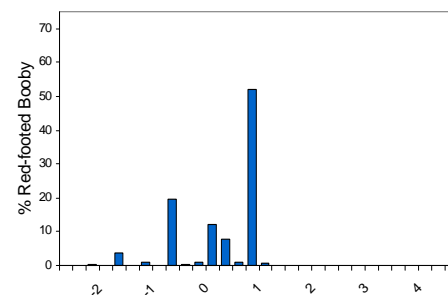
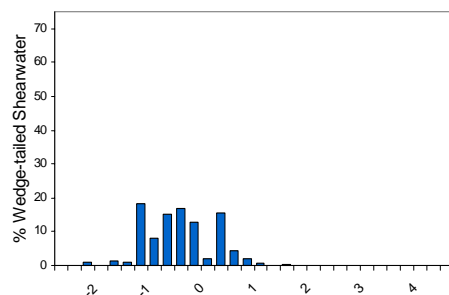
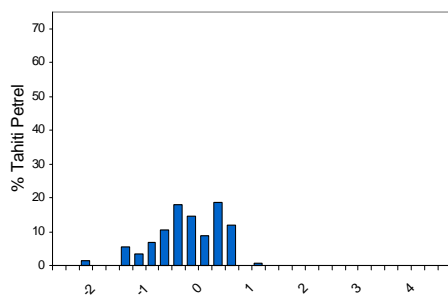
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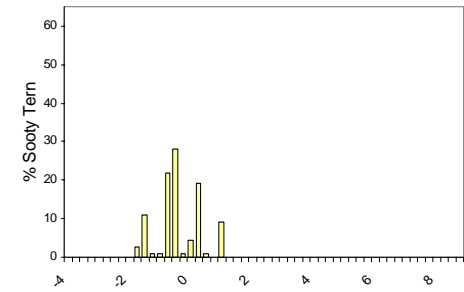
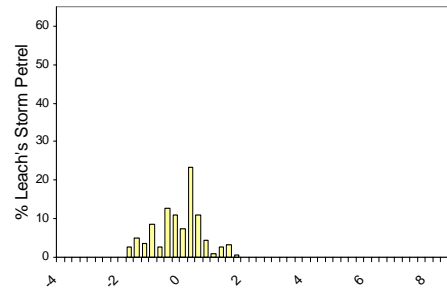
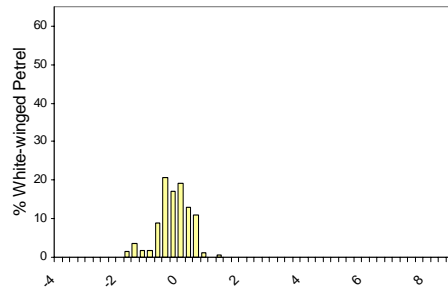
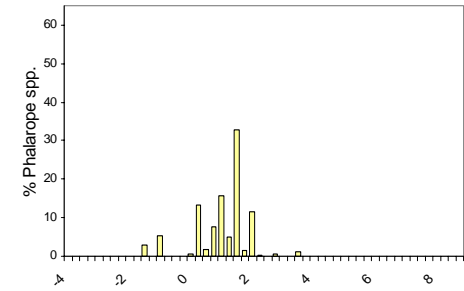
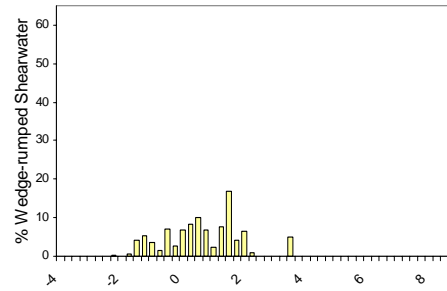
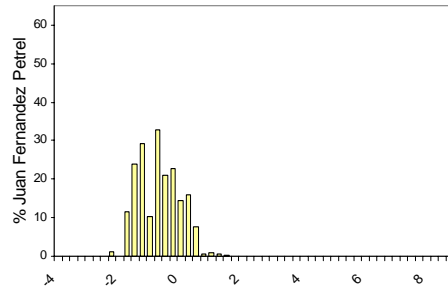
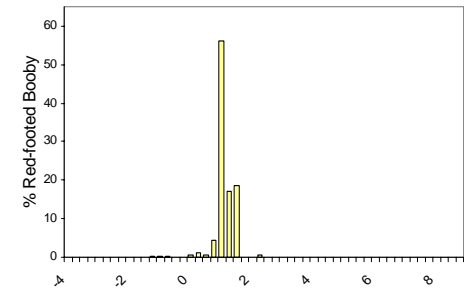
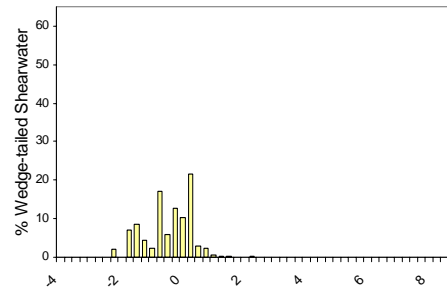
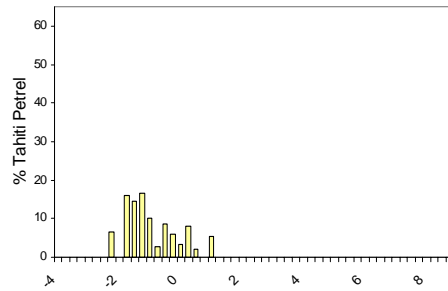
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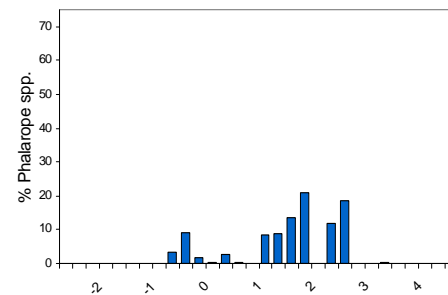
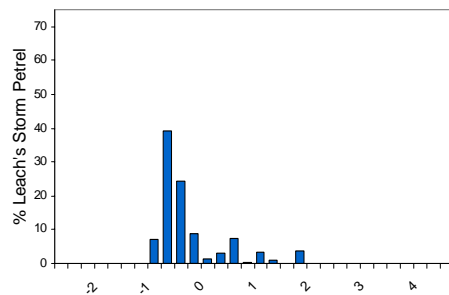
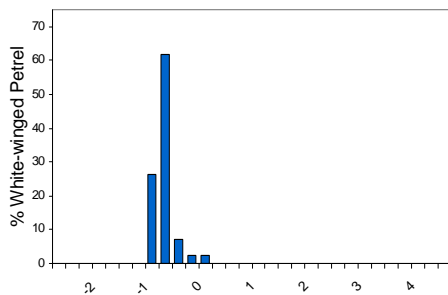
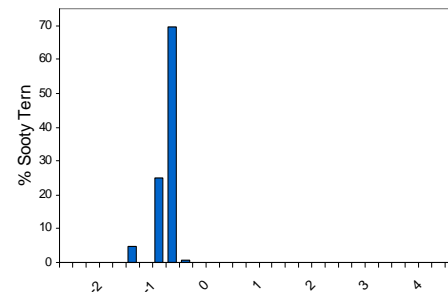
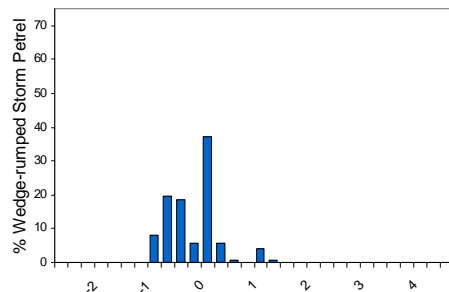
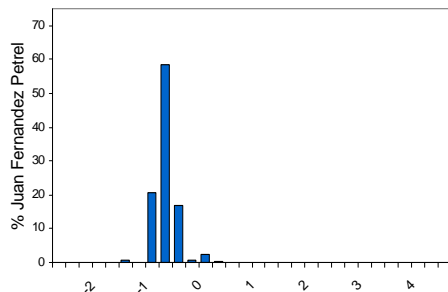
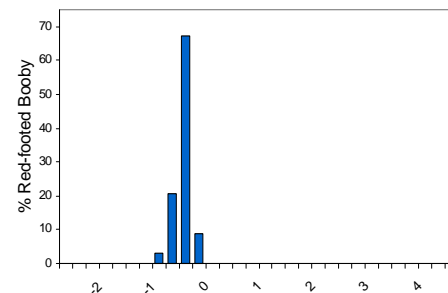
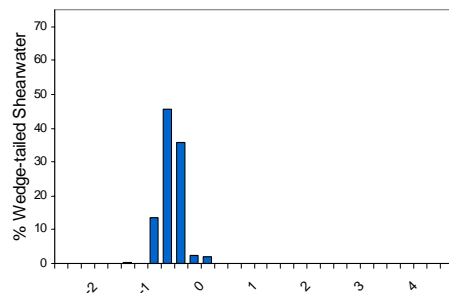
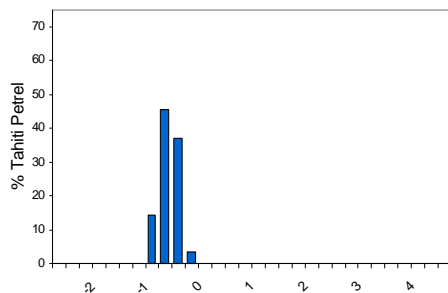
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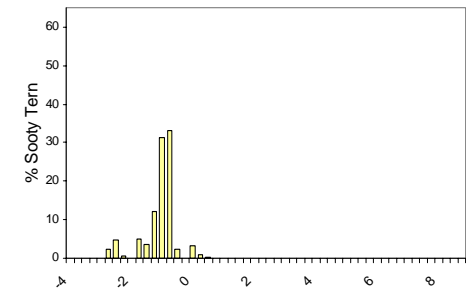
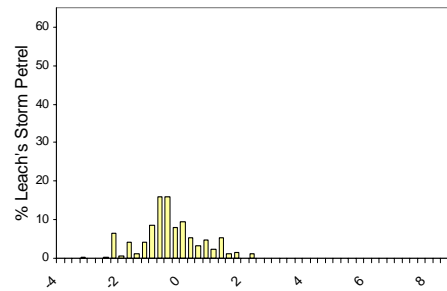
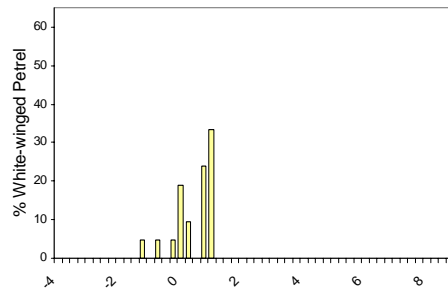
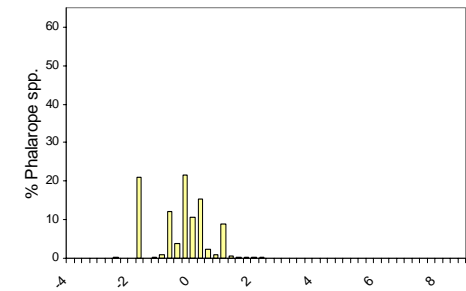
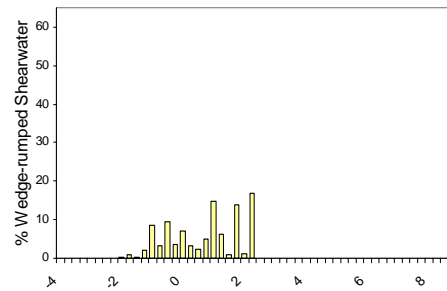
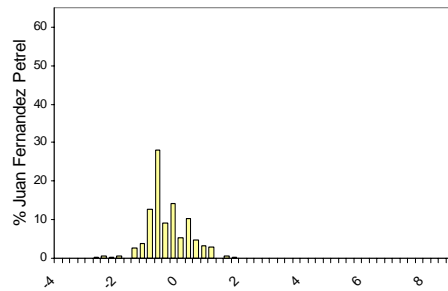
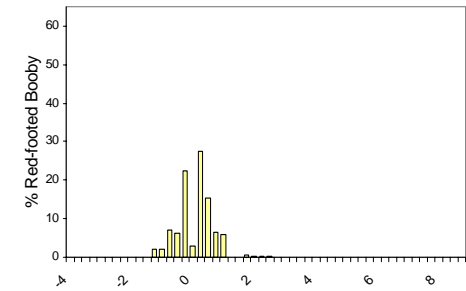
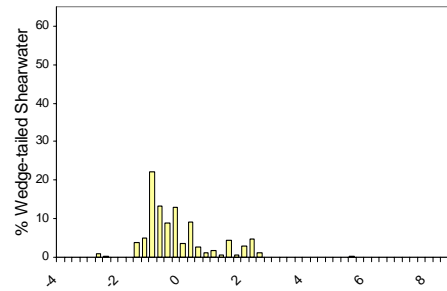
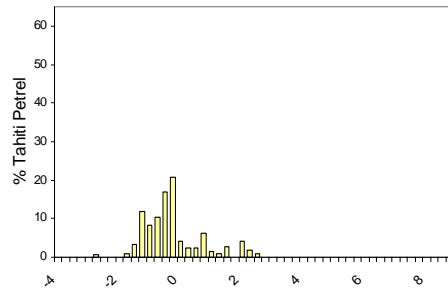
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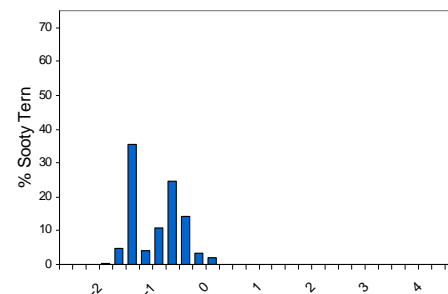
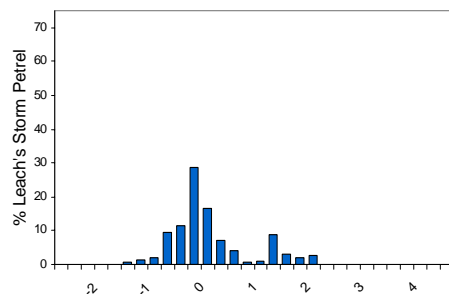
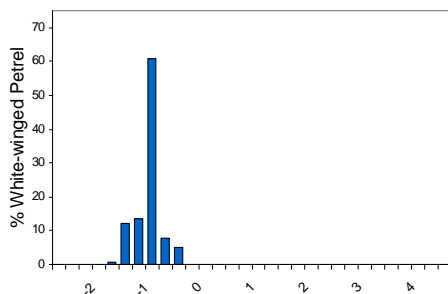
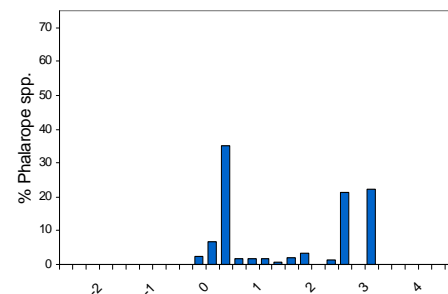
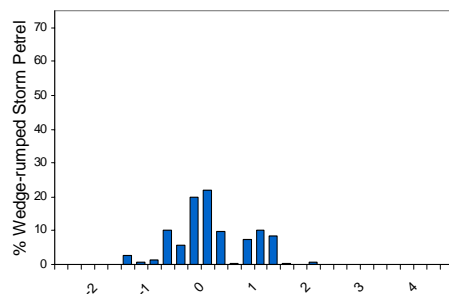
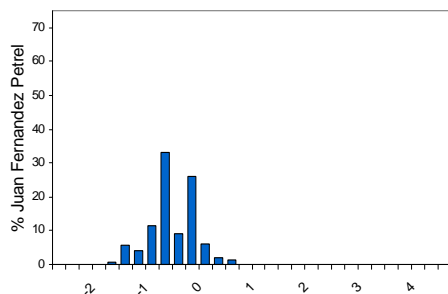
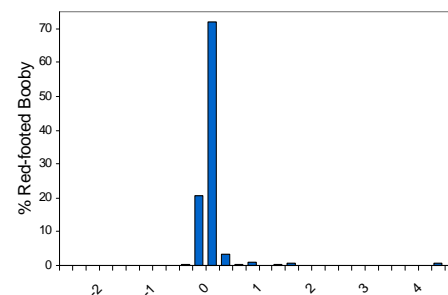
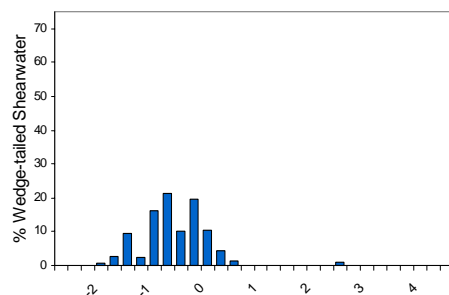
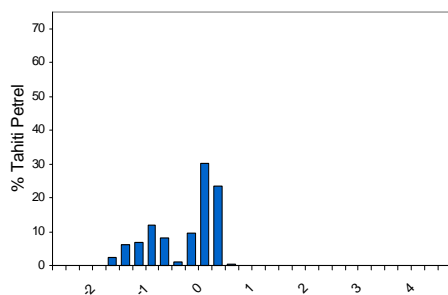
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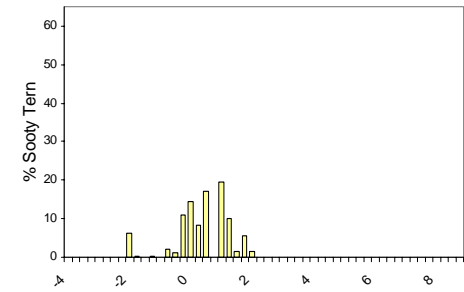
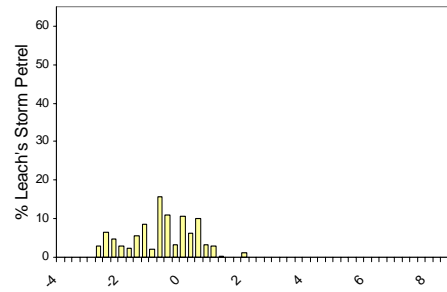
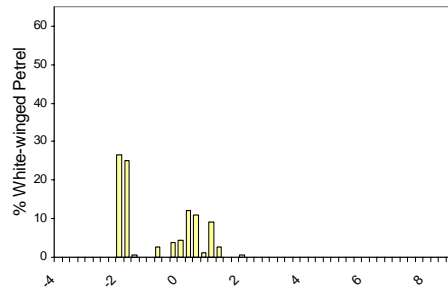
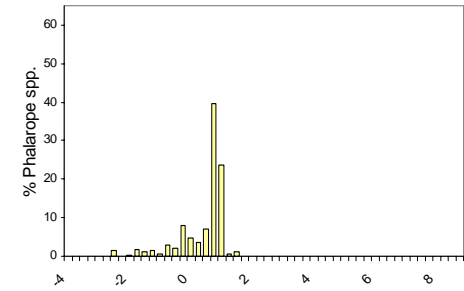
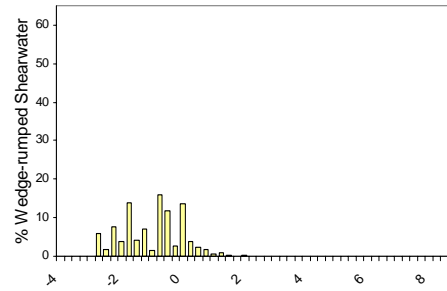
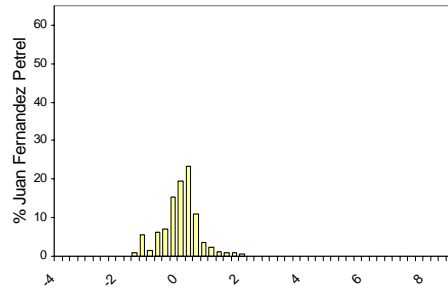
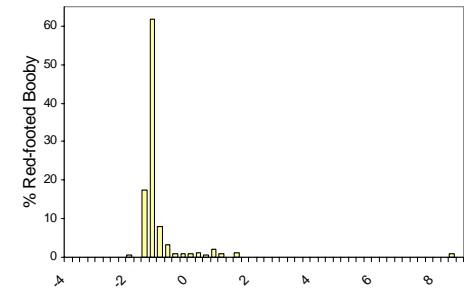
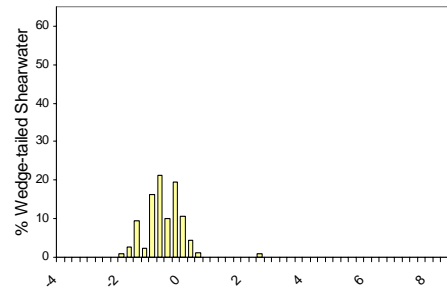
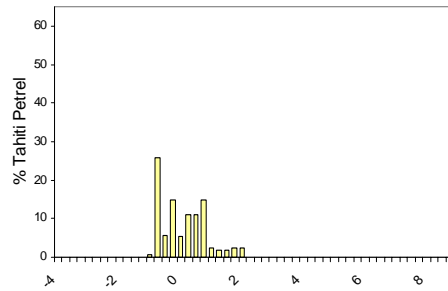
## 1998 Axis 2



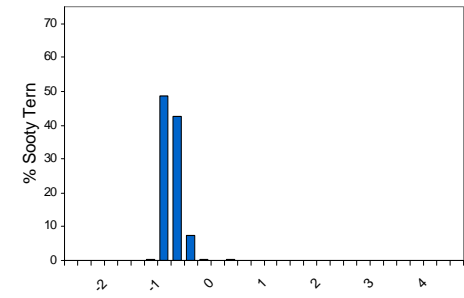
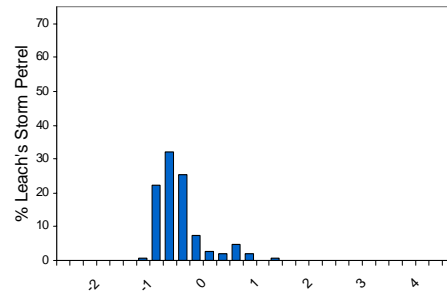
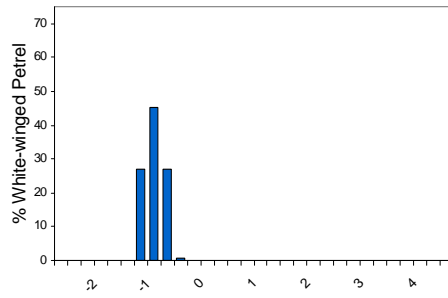
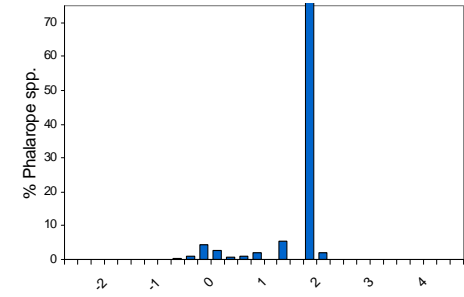
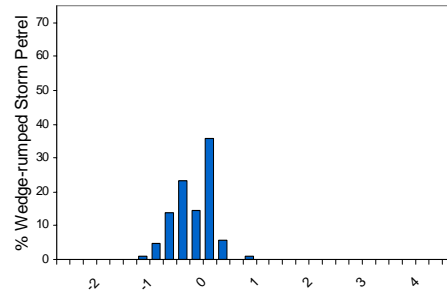
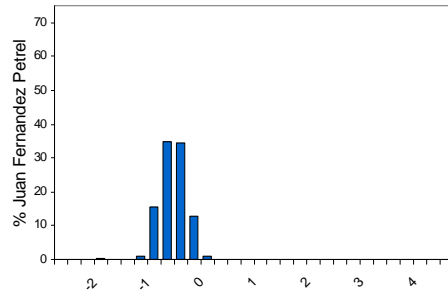
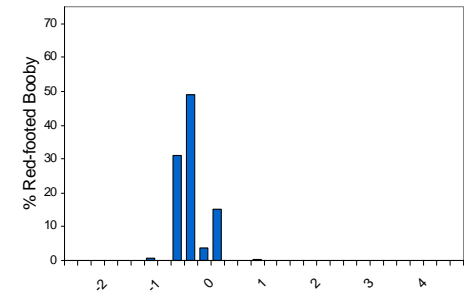
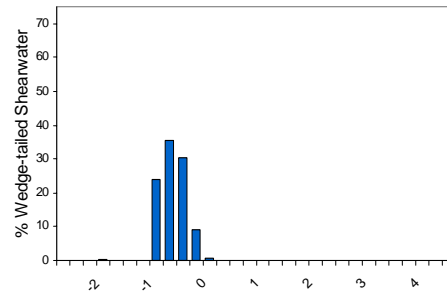
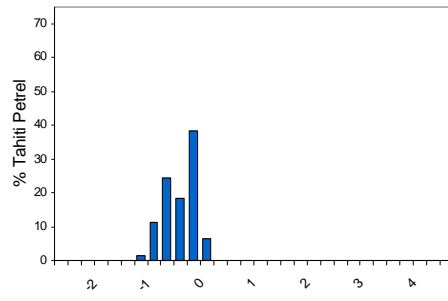
## 1999 Axis 1



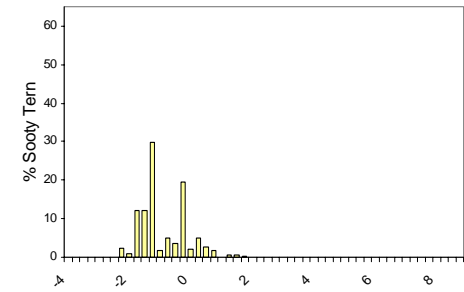
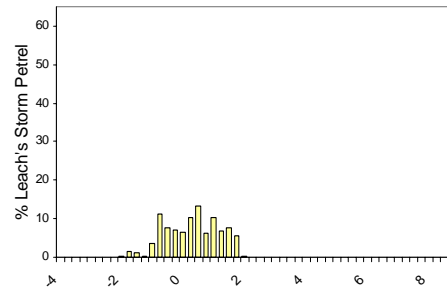
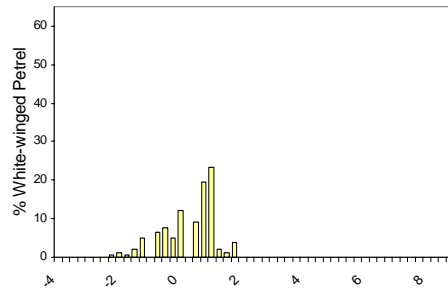
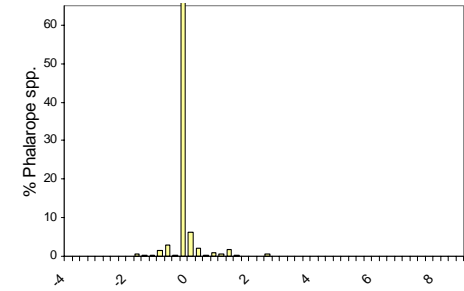
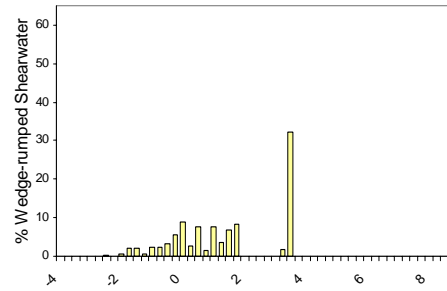
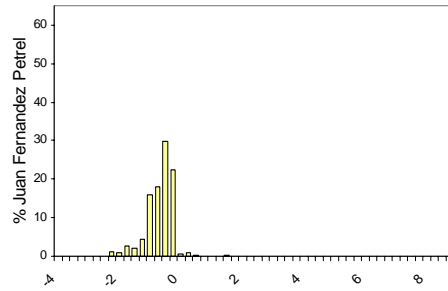
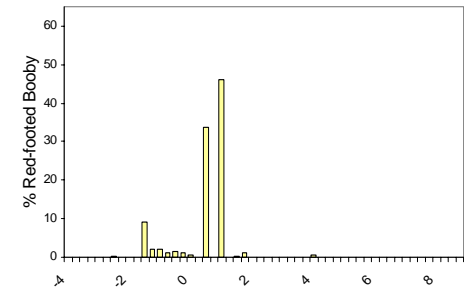
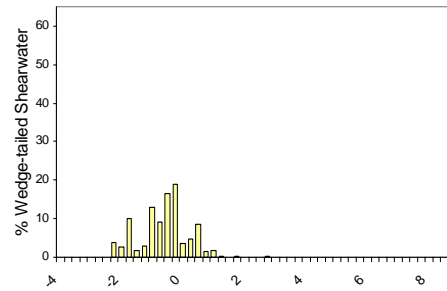
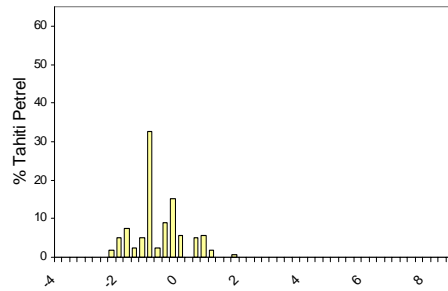
## 1999 Axis 2



## 2000 Axis 1

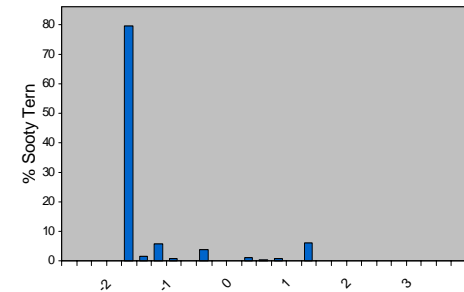
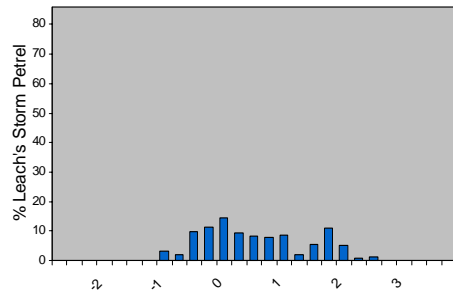
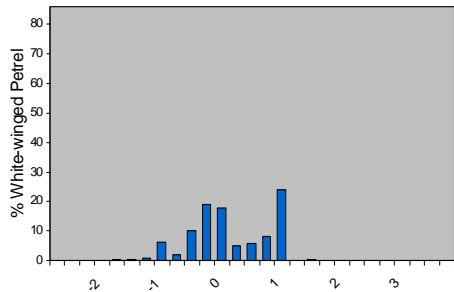
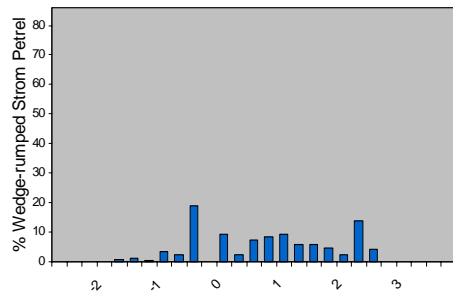
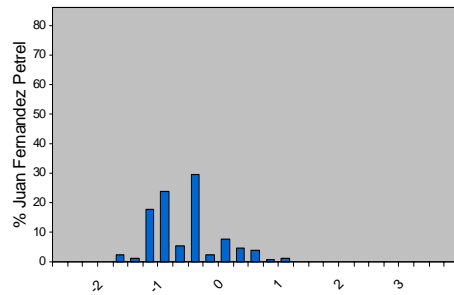
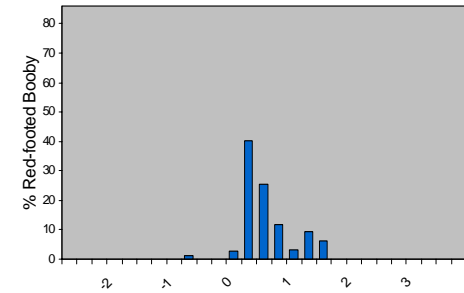
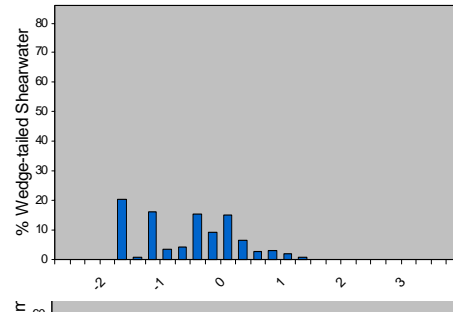
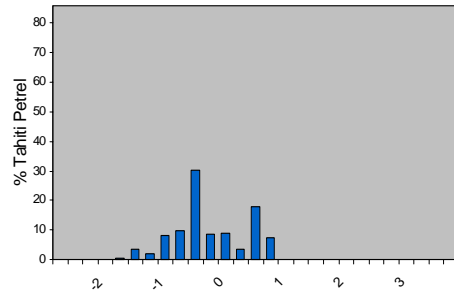


## 2000 Axis 2

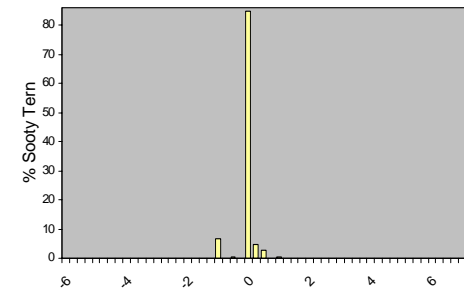
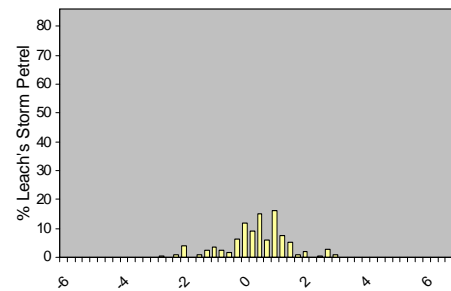
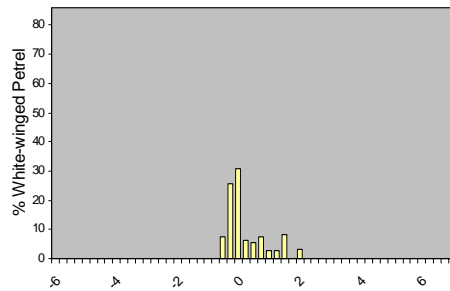
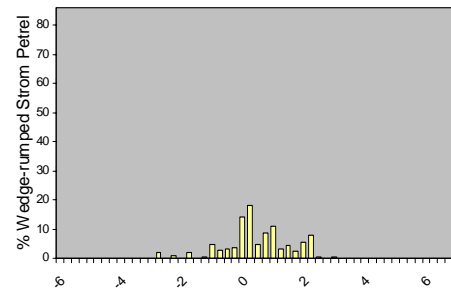
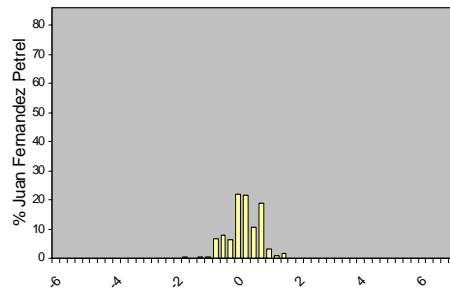
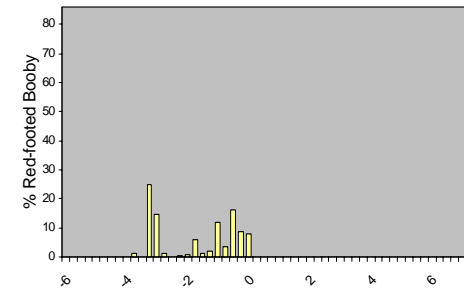
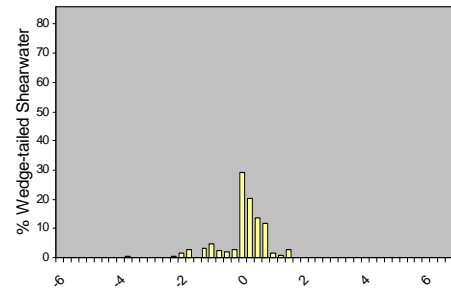
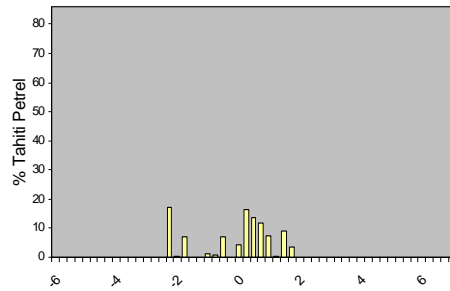


**APPENDIX 2.** Frequency histograms (by year), transformed to percentages, of the first two environmental axis scores where each of eight seabirds were sighted. (Results from eight species used in the ordination). Relationships are for the most part unimodal, thus validating an assumption of CCA.

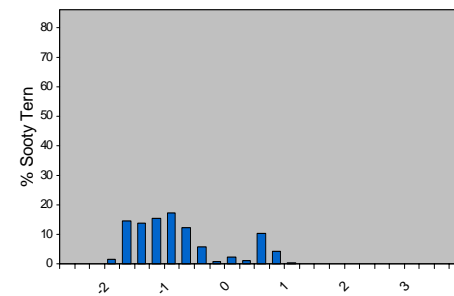
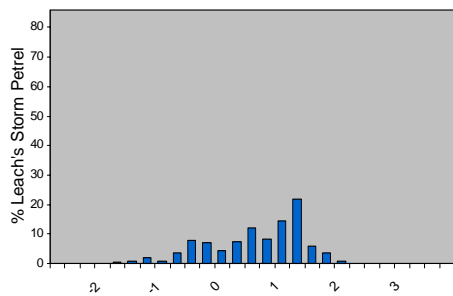
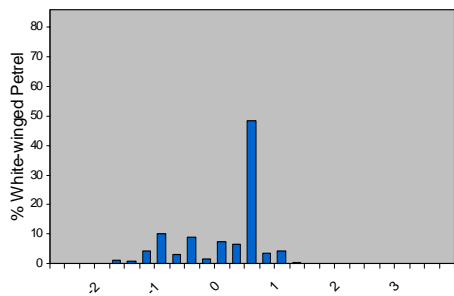
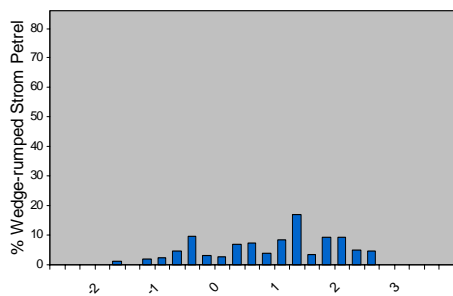
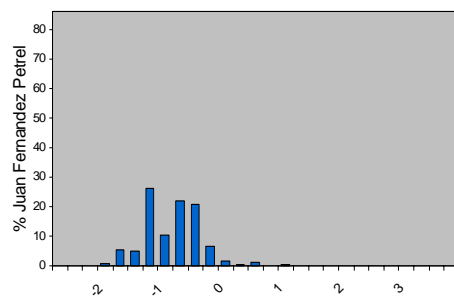
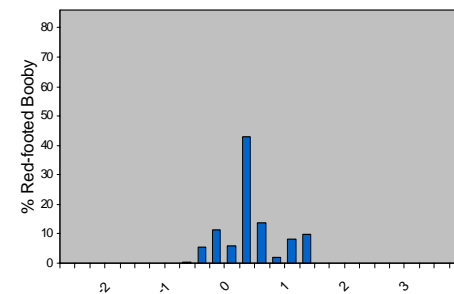
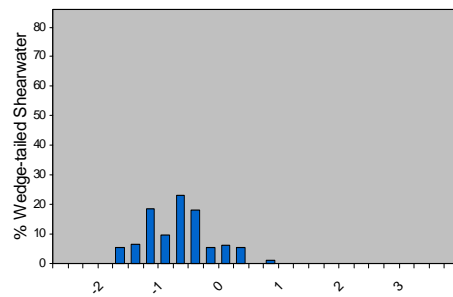
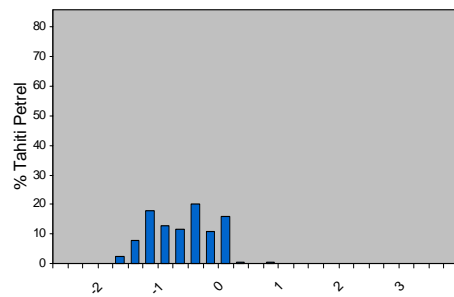
### 1988 Axis 1



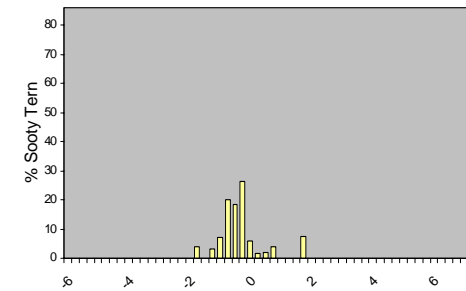
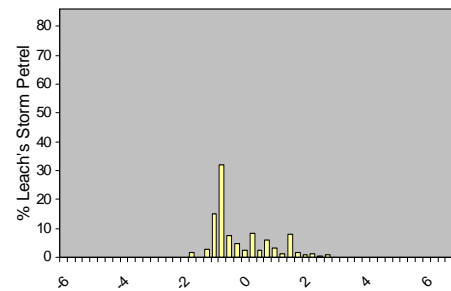
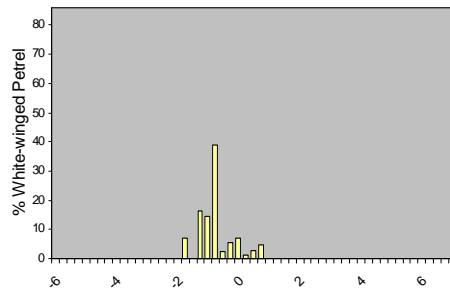
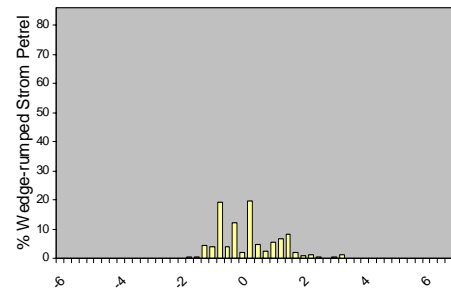
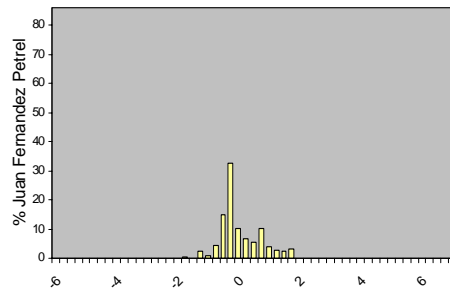
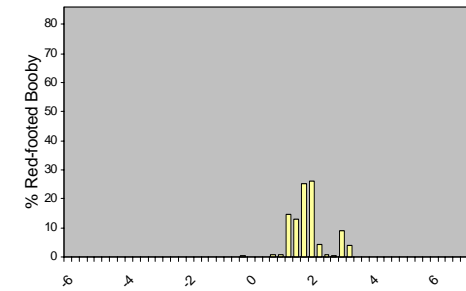
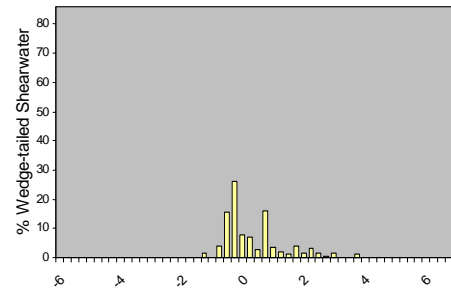
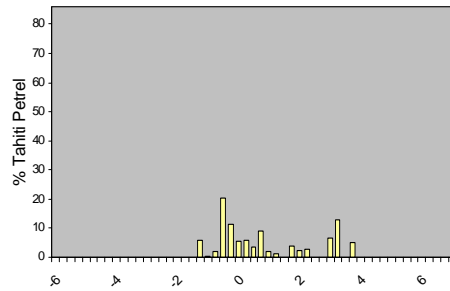
## 1988 Axis 2



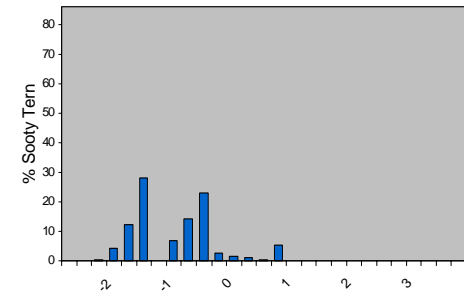
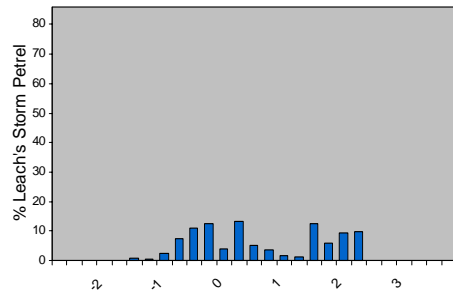
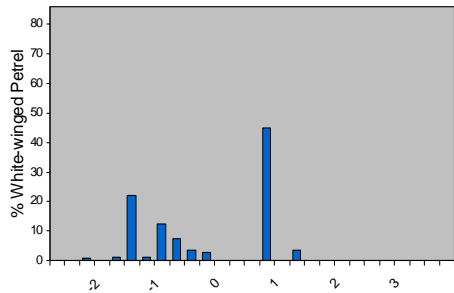
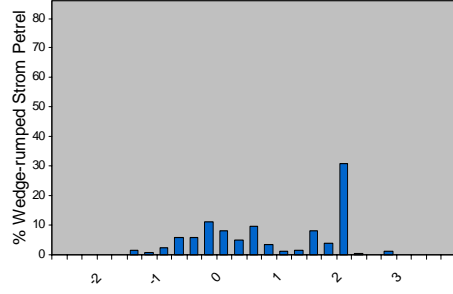
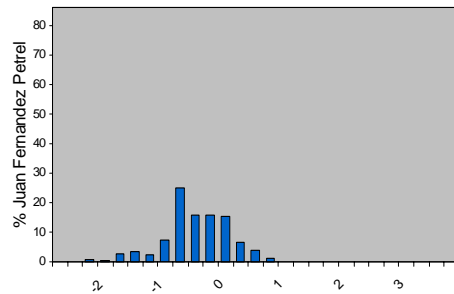
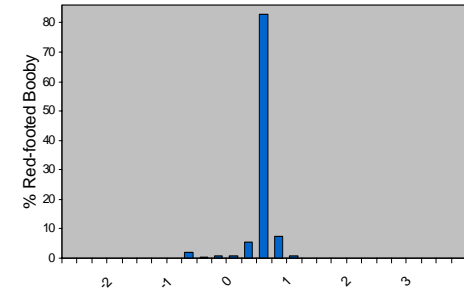
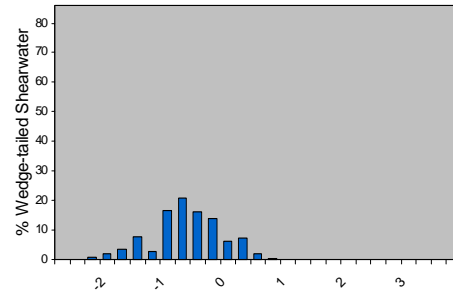
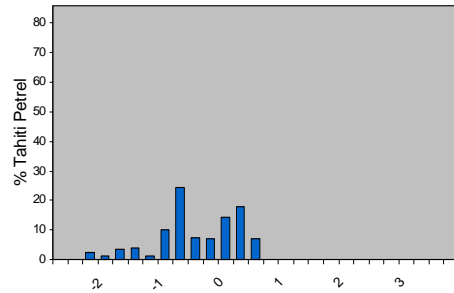
## 1989 Axis 1



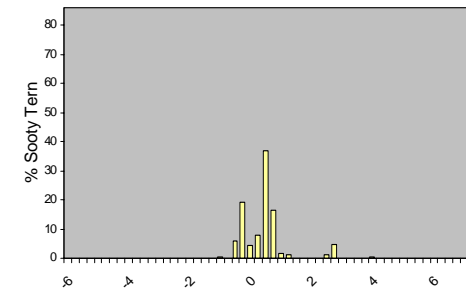
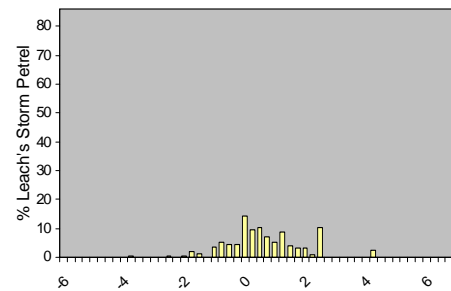
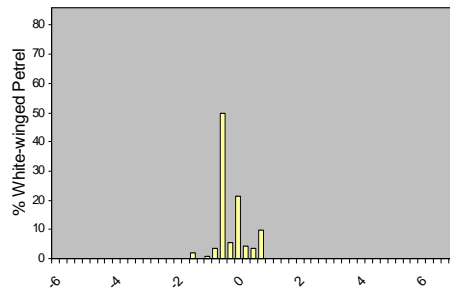
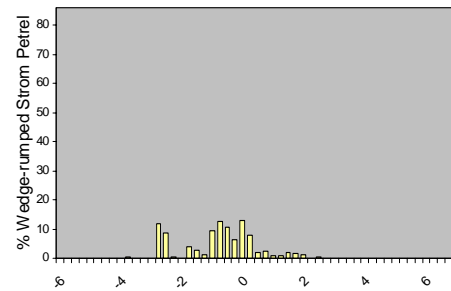
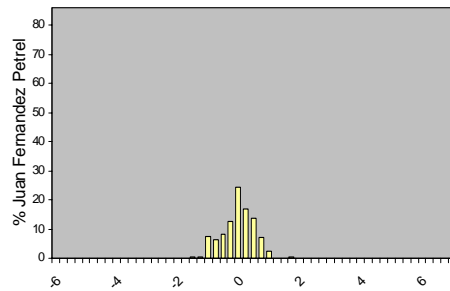
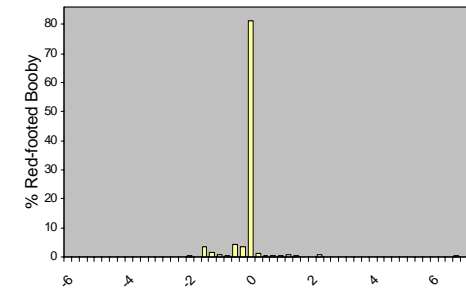
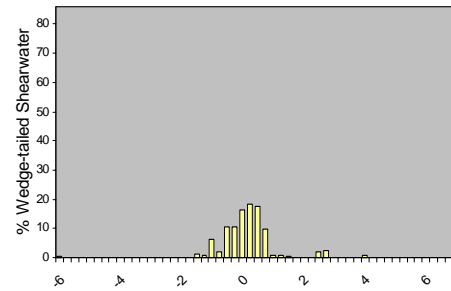
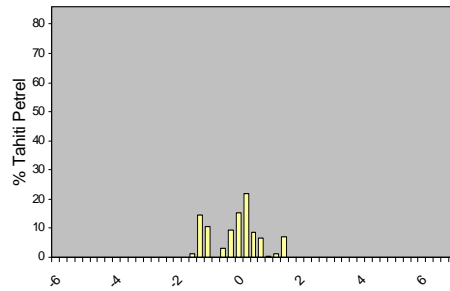
## 1989 Axis 2



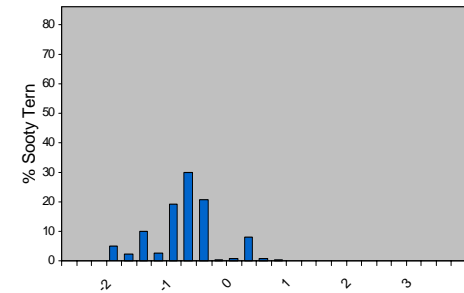
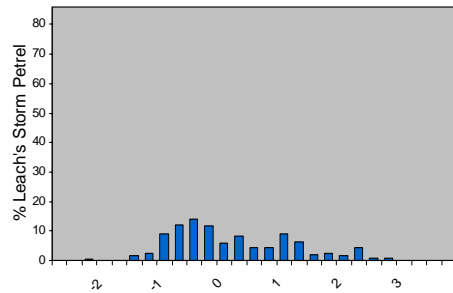
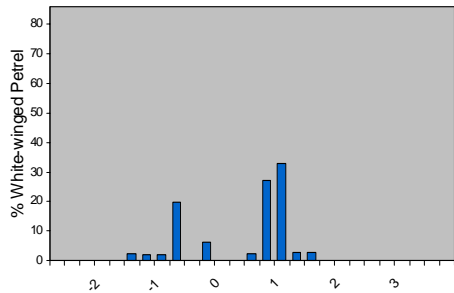
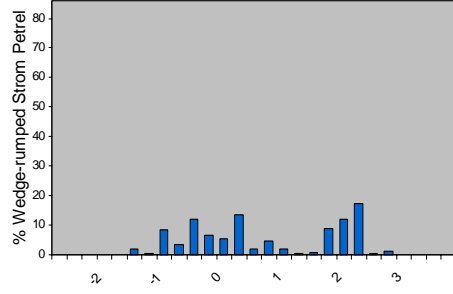
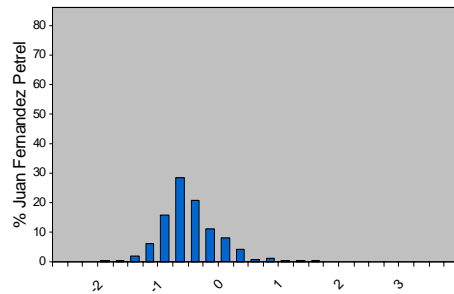
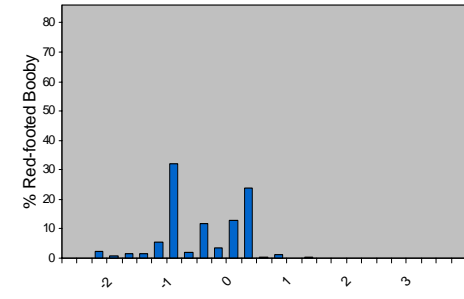
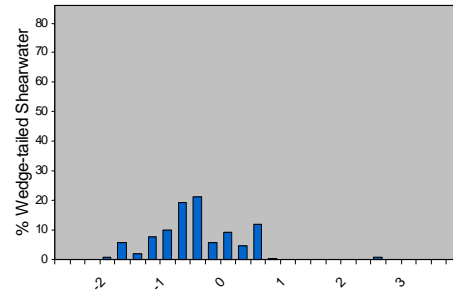
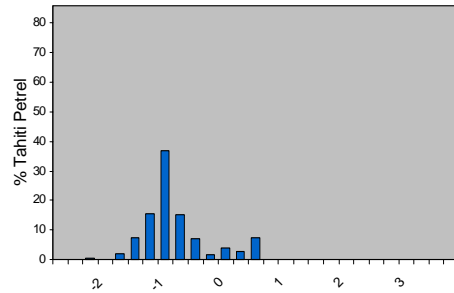
## 1990 Axis 1



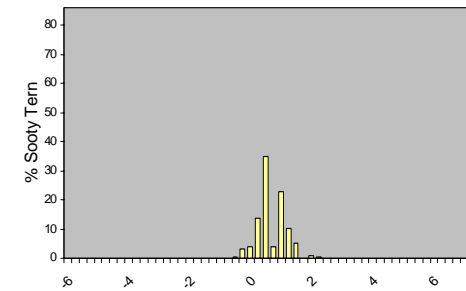
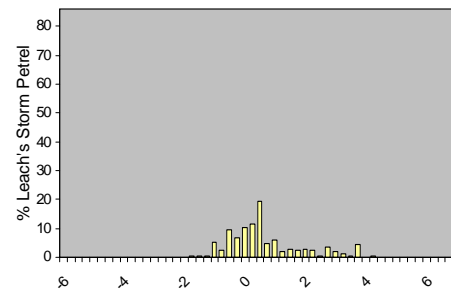
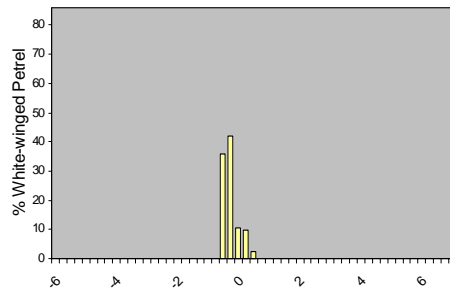
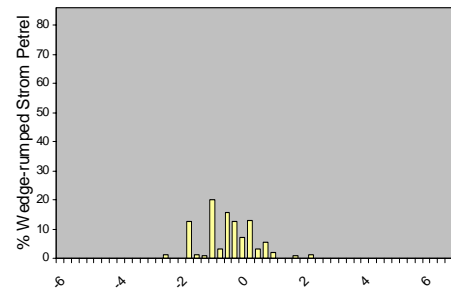
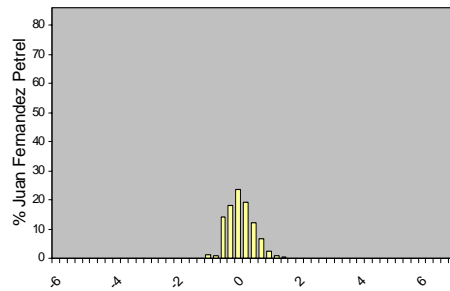
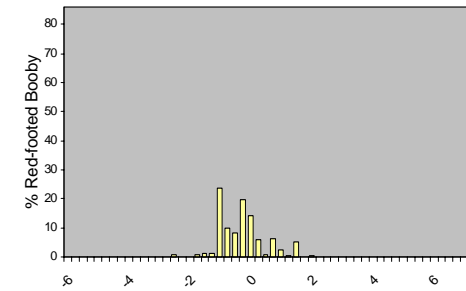
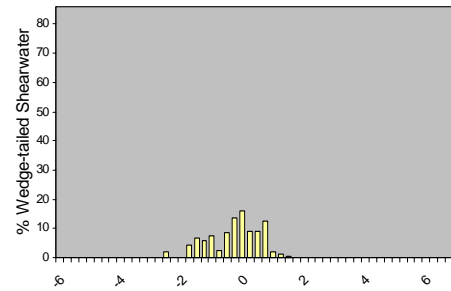
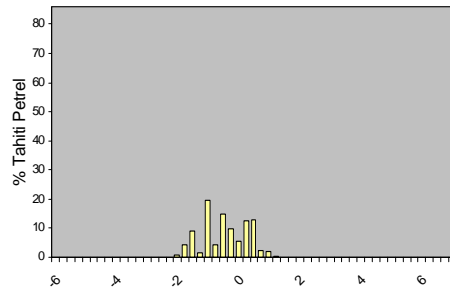
## 1990 Axis 2



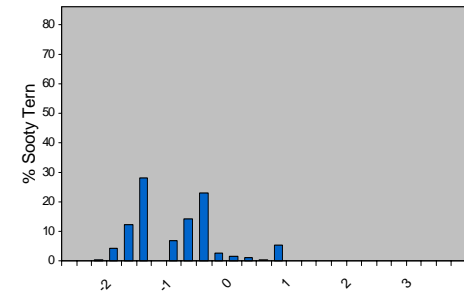
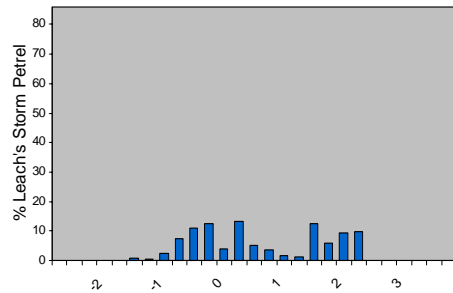
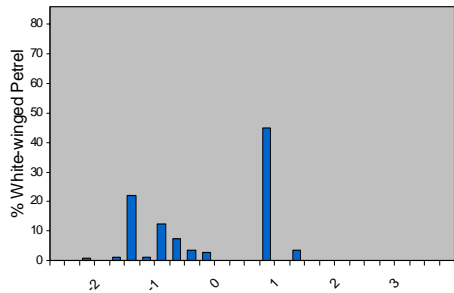
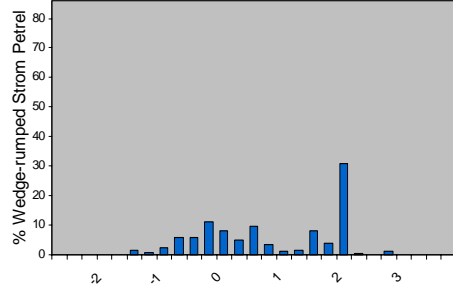
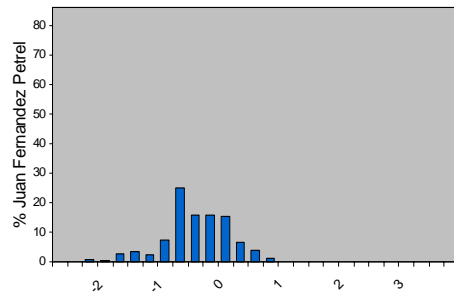
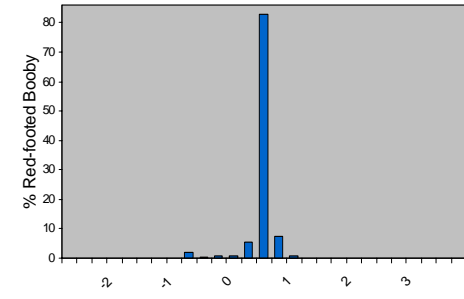
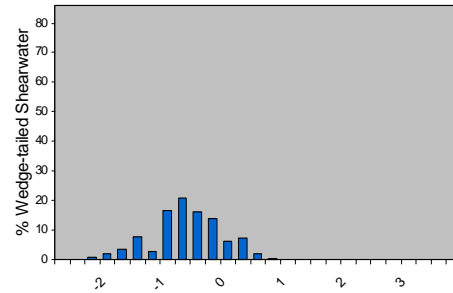
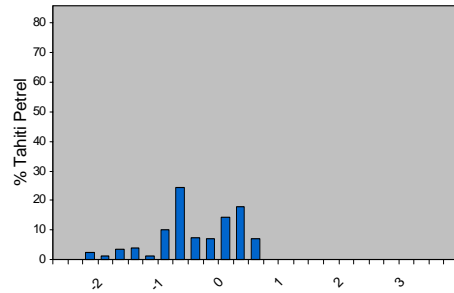
## 1998 Axis 1



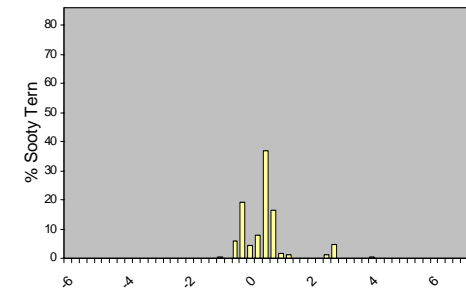
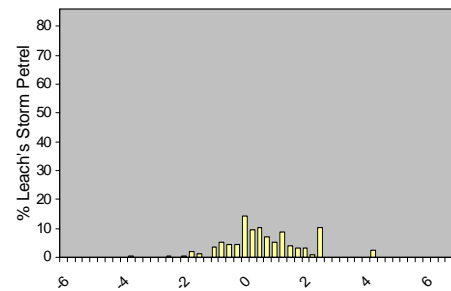
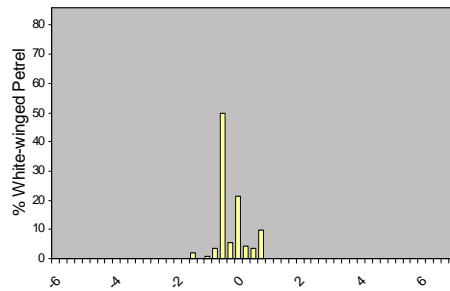
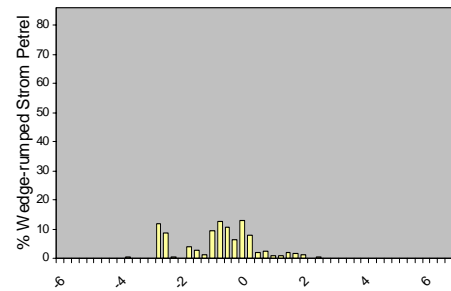
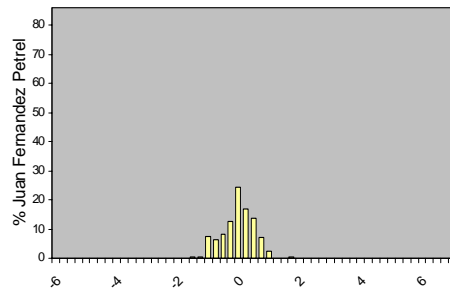
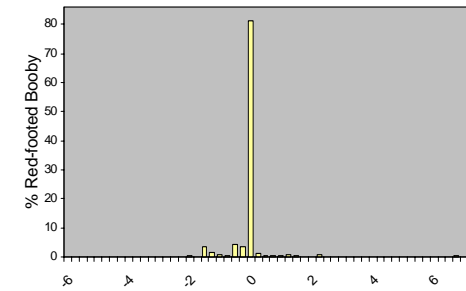
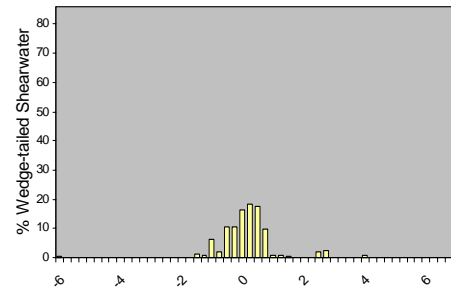
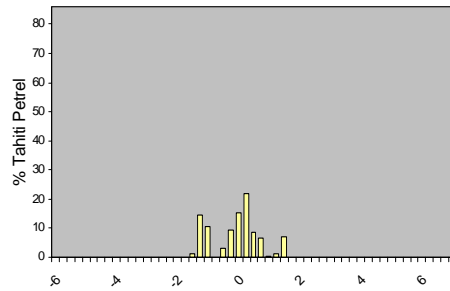
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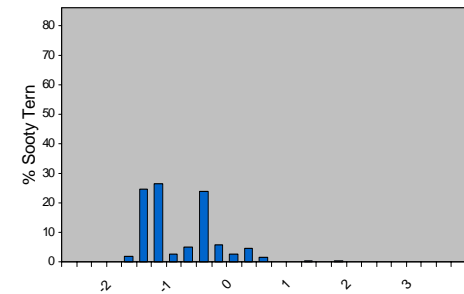
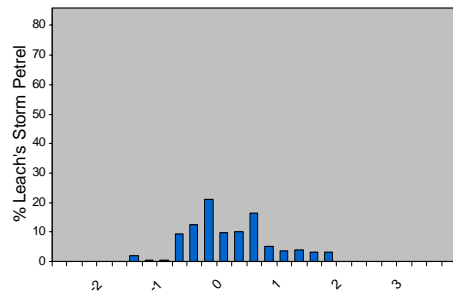
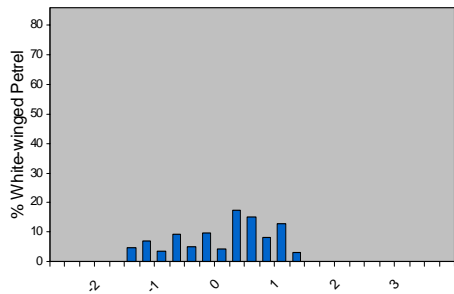
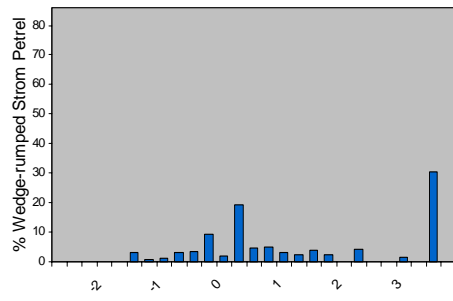
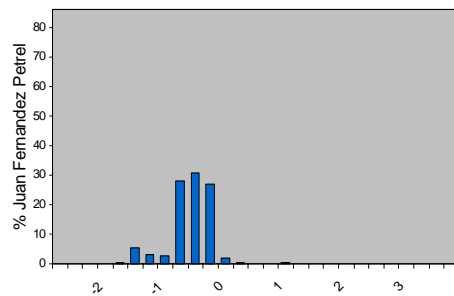
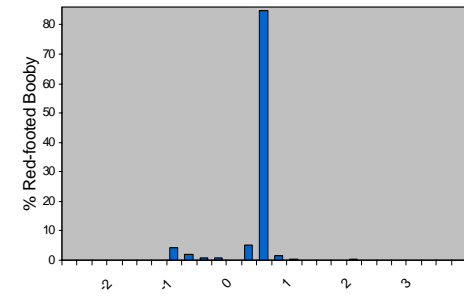
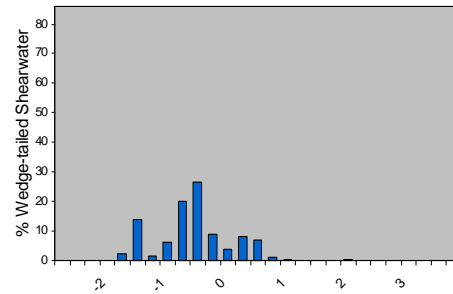
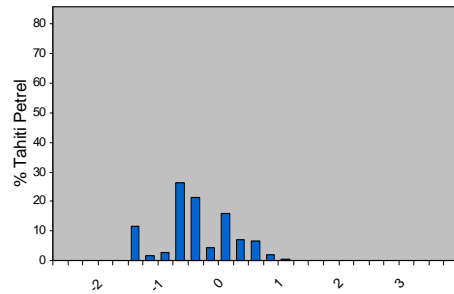
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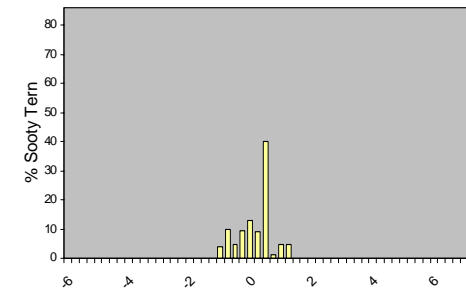
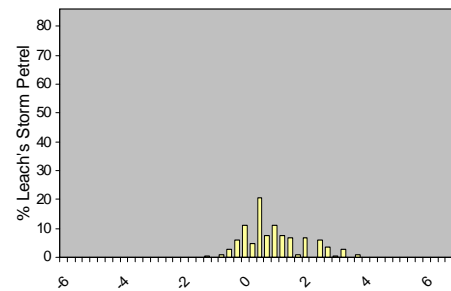
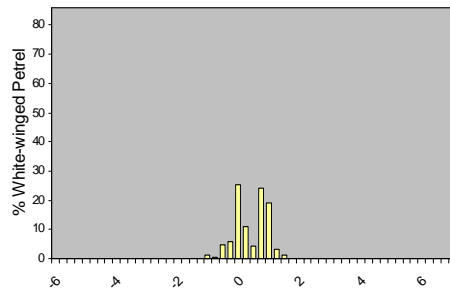
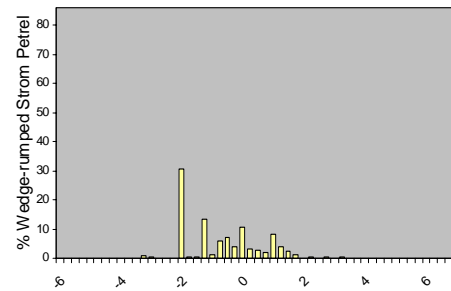
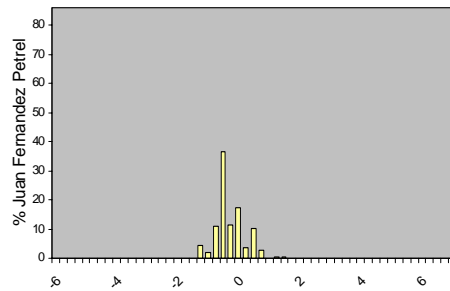
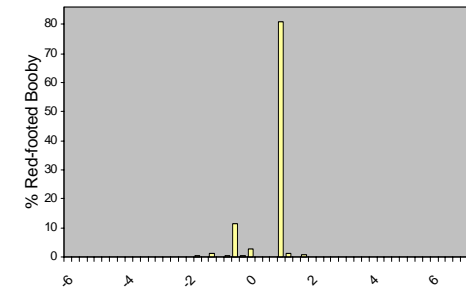
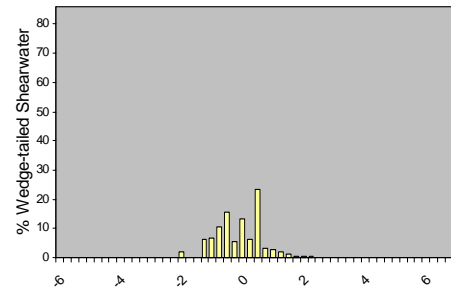
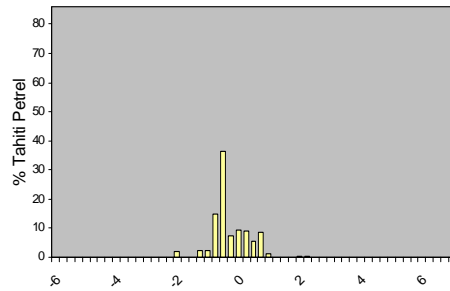
## 1999 Axis 2



## 2000 Axis 1



## 2000 Axis 2



### APPENDIX 3.

#### *Responses to recommendations provided by the Center for Independent Experts review panel*

Reviewer comments were extremely helpful and were incorporated into the current manuscript with the exception of those that fell into the categories below. The overall impression from all reviewers was that they were in agreement with the general conclusions of this paper, given the restricted time series of data available for analysis.

1. A number of reviewers made suggestions that would improve the presentation style of data or change the quantitative results, but which would not affect the qualitative conclusions of the analyses (see the following list). Due to time constraints, these suggestions were not incorporated into the present paper, but will be in future papers intended for publication in peer-reviewed journals.

Oxenford: P. 11 bullet 3.

Drinkwater: P. 5 bullets 1 and 2; P. 13 par. 2.

Thompson: P. 11 item 5.

2. A number of valuable suggestions for additional analyses, using data not incorporated into the present paper, were made (see the following list). In particular, all reviewers placed strong emphasis on efforts to recover data collected by EASTROPAC cruises and to incorporate these into investigations of temporal patterns. Time constraints prohibit this at present, though efforts to recover these data are on-going and future investigations will include them.

Hunt: P.9 par 2; P. 13 items 2 and 3.

Oxenford: P. 16 bullet 1; P. 17 bullet 1.

Dower: P. 17 recommendation 3.

Drinkwater: P. 3 bullet 1; P. 4 bullet 2; P. 7 bullet 2; P. 13 par. 3;

Thompson: P. 8 par. 3.

3. A few reviewers suggested changes in analysis procedures for existing data, results of which may possibly change the qualitative conclusions of this research. As such, they deserve to be addressed specifically:

a) Oxenford (P. 16 bullet 4) suggests that data for all ecosystem studies be stratified into core and outer areas, and analyzed separately to look for temporal signals, particularly in the core area (key habitat of target dolphin species), that would not be confounded by spatial signals. Drinkwater (P. 6 bullet 2) and Thompson (P. 7 par. 3) make similar suggestions. We agree that this is a worthwhile approach, and in fact suggested such during the review. Time constraints do not allow such an approach to be incorporated into the current paper (the review comments were received with less than a month available to finalize ecosystem studies and have them published). We will consider such stratification in future investigations. We do note however that oceanographic analyses indicate that temporal variation in the core area is much damped relative to the entire tropical Pacific (Fiedler 2002). If organisms have distribution and abundance patterns that reflect oceanographic conditions,

as results of this paper indicate, the qualitative conclusions of analyses from the core area alone should be similar to conclusions reached in the current paper.

b) Dower (P. 17 recommendation 4) suggests that authors should explore whether the application of distribution-free statistical methods might offer a way to better deal with some of the sparse data series. Drinkwater (P. 20 bullet 1) makes a similar suggestion to use rank correlations. (These comments are presumably aimed at most or all of the ecosystem studies components.) We agree that this is a worthwhile exercise. Time constraints prohibit such investigations from being incorporated into the current paper, but we will consider this in future analyses.

c) Drinkwater (P. 7 bullet 1) suggests that additional analyses be performed with respect to temporal patterns in variability of various parameters (in addition to mean measures, which are currently incorporated). (This comment is presumably aimed at most or all of the ecosystem studies components.) This is a valuable suggestion and we intend to include such investigations in future analyses. Time constraints prohibit this approach from being incorporated into the present paper.

4. Finally, one comment was based on erroneous assumptions. We provide clarification here:

a) Drinkwater (Pp. 5-6) states that oceanographic fronts and the Costa Rica Dome are important physical features to dolphins and seabirds and suggests that greater focus be placed on analyses of these features. With respect to seabirds, these assumptions are not precisely correct. The Costa Rica Dome is an area of thermocline doming due to a cyclonic eddy produced, in part, by Equatorial Countercurrent flow being deflected by the central American continent (see Fiedler, P.C. 2002. The annual cycle and biological effects of the Costa Rica Dome. *Deep Sea Research* 49:321-338.). The cool water and relatively high surface chlorophyll are believed to be important habitat for blue whales (*Balaenoptera musculus*) and common dolphins (*Delphinus delphis*; See Reilly, S. B. and V. G. Thayer. 1990. Blue whale [*Balaenoptera musculus*] distribution in the eastern tropical Pacific. *Marine Mammal Science* 6(4):265-277. and Reilly and Fiedler 1994 [full reference in Literature Cited section], respectively), but extensive data and analyses have not indicated that the target species of dolphins are found here in any great abundance, nor do seabirds associate with this feature. The Equatorial Front is important to a number of seabirds (see Spear *et al.* 2001 [full reference in Literature Cited section]), but not to those which associate with target species of dolphins and yellowfin tuna captured by the fishery. Thus, the “tuna-dependent” seabird species in this paper are not attracted to this front and detailed investigation of it will provide no additional insights into temporal patterns in this community.